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NATURAL HISTORY OF THE PALLID BAT, *ANTROZOUS PALLIDUS* (LeConte)

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Introduction and Acknowledgments

So little is known regarding the natural history of many of our common species of North American bats that it is frequently difficult or impossible to provide satisfactory answers to seemingly simple questions on the subject. These voids in our knowledge do not reflect a lack of scientific interest in bats but rather have resulted from the technical difficulties involved in studying these animals.

Almost every above-ground movement of many kinds of diurnal mammals can be noted by careful observers. The use of live traps and of marking has provided us with considerable information on the activities of many nocturnal, terrestrial species. Who, however, can accurately state how far a bat flies in the evening after it emerges from its daytime retreat? So far as the observer is concerned the animal's identity is usually lost in the gloom of twilight within a matter of seconds. The distance that it travels in search of food, whether a few hundred

yards or some miles, must largely remain a matter for conjecture until more advanced techniques for study are developed.

Vaguely aware of some of the difficulties involved in a project concerning chiropteran life history, the writer began such an undertaking in May, 1947. The pallid bat, *Antrozous pallidus* (LeConte), was the species selected for this purpose for several reasons. It is relatively common in central California. It can easily be kept in captivity. It is sufficiently large and distinctive in appearance to be readily recognizable in the field, even at night in the beam of a flashlight. The results obtained to date are presented in this paper. These include field observations, information derived from studies of bats in captivity, and relevant data extracted from the literature. It is felt that there are still many voids in our knowledge of events concerning the natural history of this one species but it is to be hoped that future studies may solve some of these problems.

Many persons contributed to this project. I wish to thank Dr. Robert C. Miller, director of the California Academy of Sciences, for the funds and facilities provided by that institution which made this undertaking possible. I am particularly indebted to Miss Mary Louise Perry for her painstaking care of captive animals during a period of over four years and for accurately recording and interpreting data obtained from laboratory studies. I am also especially grateful to Mr. Eben McMillan for his enthusiastic cooperation in locating bat colonies in San Luis Obispo and Kern counties, California, and for his very active participation in much of the field work. For the identification of many ectoparasites and of insects used as food by bats I wish to thank Dr. Edward W. Baker, United States Department of Agriculture, Washington, D. C.; Professor G. F. Ferris, Stanford University; Mr. Robert Holdenried, United States Public Health Service, Santa Fe, New Mexico; Dr. Glen M. Kohls, United States Public Health Service, Hamilton, Montana; Mr. Frank Prince, United States Public Health Service, San Francisco, California; Dr. Edward S. Ross, Dr. Edward L. Kessel, and the late Dr. Edwin C. Van Dyke of the Department of Entomology, California Academy of Sciences. For permission to borrow or study specimens under their care I wish to thank Dr. Seth B. Benson, Museum of Vertebrate Zoology, University of California; Dr. William H. Burt, Museum of Zoology, University of Michigan; Dr. David H. Johnson, United States National Museum; and Dr. Colin C. Sanborn, Chicago Natural History Museum. Others who contributed to this study include Mr. Lionel Berryhill, Mr. Sterling Bunnel, Miss Laura Grainger, Mrs. J. Gordon Irving, Mrs. Berta B. Kessel, Mr. Hugh B. Leech, Mr. Ian McMillan, Mrs. Dorothy B. Orr, Mr. Frank L. Rogers, Dr. Charles G. Sibley, Mr. Leon E. Salanave, and Mr. M. Woodbridge Williams.

METHODS

A number of summering colonies of pallid bats were known to the writer in or fairly close to the San Francisco Bay region. Most of the field work, however, was concentrated in eastern San Luis Obispo and western Kern counties because conditions in that region seemed highly favorable for bats of this species, judging from their abundance, and because the environmental changes resulting from human usage had been less there than in many parts of California.

Thirty-one days, devoted primarily to obtaining data relevant to this species, were spent in the field as follows:

May 9–11, 1947, San Luis Obispo and Kern counties.

August 9–10, 1947, Humboldt County (M. L. Perry).

September 19–22, 1947, San Luis Obispo and Kern counties.

February 27–March 1, 1948, Monterey, San Luis Obispo, and Kern counties.

June 5–9, 1948, San Luis Obispo and Kern counties.

April 1–4, 1949, Monterey, San Luis Obispo, and Kern counties.

October 21–24, 1949, Monterey, San Luis Obispo, and Kern counties.

January 22, 1950, Marin County.

April 13–16, 1951, San Luis Obispo and Kern counties.

June 13, 1952, Santa Clara County.

Although all of the field observations made on *Antrozous pallidus* were within the range of the race *pacificus,* as given by Grinnell (1933), occasional references are made to published reports concerning the natural history of other geographic forms of this species.

Pallid bats were maintained in captivity during the entire period of this study. Most of the wild-taken individuals were released, with United States Fish and Wildlife Service bird bands attached to their forearms, from 10 to 13 months after capture. Such releases were made either at the original place of capture or, for experimental purposes in an attempt to study homing instinct, at some other locality within the same general region in which field studies were made.

As a rule bats were captured at their daytime retreats, usually with the aid of insect nets and long-handled forceps. They were transported to the laboratory in cages 16 inches wide, 16 inches high, and 12 inches deep, made of plywood and quarter-inch hardware cloth, with sliding doors at the back. At the California Academy of Sciences bats were housed in several sizes of cages for various purposes. Small retaining cages of the type just mentioned were used for the confinement of females with newly born young to facilitate studies on behavior and

growth, for isolating certain individuals, and in enforced dormancy experiments. A larger cage, 48 inches wide, 38 inches high, and 42 inches deep, made of quarter-inch hardware cloth on a wooden frame, was used for small colonies kept in the laboratory. This was sufficiently large to permit limited flight. Two large flight cages, 4 feet wide, 8 feet high, and 10 feet deep, that had previously been used as aviaries (for detailed description see Orr, 1945, p. 179) on the roof of the Academy's North American Hall, served to maintain small colonies of bats out-of-doors.

The smaller cages were kept darkened during the day by hanging burlap or paper over the screened side or by placing this side next to a wall. In the larger cages bricks, boards, or small boxes provided daytime retreats for the bats. Each occupied cage was provided with food and water daily, except on week-ends. The food consisted principally of meal worms (the larvae of the flour beetle, *Tenebrio molitor*) which were killed by momentarily scalding them before they were placed in the feeding dishes in the late afternoon. Since, on occasion, as many as 10,000 meal worms were used weekly, it was not found practical to raise them. They were secured from the Sure-Bite Live Bait Company in Torrance, California.

Toward the end of this project it was found more practical, economical, and satisfactory from the standpoint of maintaining healthy captive animals, to use a food mixture recommended by Mr. Ernest P. Walker, assistant director of the National Zoological Park, Washington, D. C. This consisted of equal parts of hard-boiled egg yolk, cottage cheese, ripe banana, and meal worms, with small amounts of Jeculin, wheat germ oil, and vitamin mixture added. The ingredients were ground into a paste. It was found expedient to prepare a fairly large quantity of this food at one time, dividing it into small portions which were wrapped in wax paper and kept frozen until needed.

Description

The pallid bat is readily distinguished, on the basis of external characters, from all other North American bats by its combination of large size, proportionately large ears and broad wings, peculiar shape of nose, and color of pelage.

Of the 24 species of bats recorded as occurring in California (Grinnell, 1933; Constantine, 1946; Olson, 1947) only 4 approximately equal or exceed the pallid bat in general body size. These are the hoary bat (*Lasiurus cinereus* (Beauvois)), the western yellow bat (*Dasypterus ega* (Gervais)), the pocketed bat (*Tadarida femorosacca* (Merriam)), and the mastiff bat (*Molossus perotis* Schinz). The hoary bat is not often

Figure 1. The ears and eyes of the pallid bat are proportionately large. Note the serrated outer edge of the tragus. Photographed at the California Academy of Sciences, November 12, 1952.

found in the same region as the pallid bat, except in spring and autumn when the former species is migrating. Only once during this study were these two species noted together (Orr, 1950). The western yellow bat has been recorded only once from California (Constantine, 1946). The pocketed bat and the mastiff bat are both members of the family Molossidae. The former species is very rare in California, known only from the extreme southern part of the state. The mastiff bat is more widely distributed but of rather local occurrence and cannot be considered common. Furthermore, it is readily distinguished from the pallid bat by its greater size, having an average wingspread in excess of 500 millimeters.

The ears of the pallid bat are separate and large, although not as long, proportionately, as in members of the genera *Corynorhinus* and *Euderma*. In shape the pinna is roughly rhomboidal, obliquely attached at the base and rounded at the tip. When laid forward it extends considerably beyond the nose. Along the postero-lateral half of the ear there are usually 9 to 11 horizontal creases which permit the pinna to be folded back. The tragus is slender, tapering distally, rounded at the tip, and serrate along the outer edge (fig. 1). The ears are pale grayish tan in color. A narrow strip of hairs is present on the antero-dorsal rim

of the pinna, extending from the base halfway to the tip. Two narrow bands of hairs, extending parallel to the long axis of the ear, are present inside the pinna.

The wings are proportionately broad with the third metacarpal only slightly longer than the fifth. Only the extreme tip of the tail extends beyond the uropatagial membrane. The flight membranes, in general, are essentially naked except those parts immediately adjacent to the body. In color they are a dark slate gray with a slight vinaceous tinge. The calcar terminates in a small but distinct lobe just short of the middle of the free edge of the uropatagial membrane. The feet are proportionately large and broad, with a few sparse hairs on the backs of the toes.

The end of the muzzle of the pallid bat is decidedly truncate with the nostrils opening forward. The rhinarium is scroll-shaped and elevated into a slight ridge above the nares. Behind the rhinarium, on either side of the muzzle, is a large, flattened, glandular swelling (fig. 2). The eyes are relatively large for vespertilionid bats.

TABLE I

Average and extreme measurements, in millimeters, of adult specimens of *Antrozous pallidus pacificus* from eastern San Luis Obispo and western Kern counties, California.

	Total length	Tail length	Hind foot	Ear from notch	Fore-arm	Wing-spread
			Males			
Average	115.9	39.6	13.3	29.1	56.3	383
Maximum	124	44	15	31	58.1	385
Minimum	111	35	11	27	53.3	382
Number averaged	15	15	15	14	10	3
			Females			
Average	118.7	42.6	13.7	30.1	57.9	380.3
Maximum	130	49	16	33	60.2	393
Minimum	107	37	12	26	54.2	370
Number averaged	22	22	21	22	13	9

Pelage: The fur of the pallid bat is not dense and is of moderate length and medium texture. The hairs on the dorsal surface of the body are, for the most part, longer and more widely separated from one another than are those on the ventral surface. The area between the

Figure 2. Large, glandular swellings are situated on either side of the muzzle of the pallid bat, immediately behind the scroll-shaped rhinarium. Photographed at the California Academy of Sciences, December 10, 1952.

shoulders is very scantily haired. Some of the longest hairs from the back of an average adult specimen in fresh pelage measured 8 millimeters from tip to base when taut. Owing to a slight natural kinkiness, however, the actual distance from tip to base rarely exceeds 5 or 6 millimeters for the dorsal hairs and 3 to 4 millimeters for hairs on the ventral parts of the body.

The hairs on the dorsal areas of the head and body are bicolored. In specimens of *Antrozous pallidus pacificus* Merriam from San Luis Obispo County, in fresh pelage, the distal third of these hairs is nearest Ridgway's (1912) Olive-Brown and the proximal two-thirds is nearest Cartridge Buff. The hairs on the ventral surface of the head and body are generally unicolored and, in fresh pelage, vary from a creamy white to a very pale grayish white. Occasionally some of the tips of the ventral hairs have a fuscous tinge, especially those on the posterior part of the body. In worn pelage the distal third of the hairs of the upper

parts tends to become lighter, approaching Saccardo's Umber while the proximal two-thirds of these hairs becomes more yellowish than in fresh pelage. Likewise, the hairs on the ventral parts become more buffy. A certain amount of this seasonal change in pelage color, particularly on the underside of the body, appears to be adventitious, possibly because of frequent contact with urine and excrement in the roosts.

One example of albinism is known. Setzer (1950, p. 350) records an albinistic specimen of this species in the collection of the United States National Museum. It was secured by Stanley G. Jewett on February 9, 1940, 26 miles north of Las Vegas, Nevada.

Molt: There is but one molt annually in this species. This takes place during the summer months, the time of occurrence varying considerably with different individuals in the same colony. Examination of museum specimens, captive bats, and those living in the wild failed to indicate any sign of molt starting before early May or of not having begun by the end of August. Most signs of molting were to be observed during the months of June and July. Pregnancy does not appear to influence the molt. Examination of females in late stages of pregnancy on June 6, 1948, in eastern San Luis Obispo County, showed that some had not yet begun to molt while others in the same colony were either in process of molting or had already assumed new pelage.

New pelage first makes its appearance on the relatively bare area of the back, between the shoulders, and, midventrally, at the base of the neck. The new hairs on the intershoulder area radiate from a point on the middorsal line while the new hairs on the underside of the neck are arranged in the form of a whorl. Simultaneously with the appearance of new hair on these two parts of the body the skin of the back appears darkly pigmented. Following this, new hair is soon in evidence from the crown of the head to the lower part of the back and on the ventral part of the head and body. The new hairs grow more rapidly on the middorsal surface than elsewhere and appear last of all on the front of the head, sides of the neck, and rump. Examinations of study skins as well as living individuals have shown that the old fur on a particular part of the body falls out when the new fur on that area has grown out to about half of its full length. When captive molting bats were handled at this stage the old fur came out readily in clumps.

The time required to complete the molt seemingly is not very long. One captive individual was observed in the very early stages of molt on August 26, 1949. New fur was just appearing above the surface of the skin between the shoulders and on the underside of the neck. When this bat was examined 13 days later it was completely in new pelage although some of the hairs had not yet quite attained full length.

Distribution

Antrozous pallidus belongs to the family Vespertilionidae and the subfamily Nyctophilinae. The only other genus belonging to this subfamily, according to Miller (1907, p. 234) and Simpson (1945, p. 60), is *Nyctophilus* of Australia and the East Indies. The genus *Antrozous* is restricted to North America where its range extends from southern British Columbia east to Kansas and south to south-central Mexico. It has been recorded[1] in the following states or provinces: southern British Columbia (Racey, 1933, p. 18), eastern Washington (Dalquest, 1938, p. 213), parts of Oregon (Bailey, 1936, pp. 390–392), parts of California (Grinnell, 1933, pp. 93–94), western and southern Nevada (Hall, 1946, p. 164), southern and eastern Utah (Durrant, 1952, p. 60), parts of Arizona (Miller, 1897, p. 44; Swarth, 1929, p. 347; McKee, 1932, p. 71; Cahalane, 1939, p. 422), parts of New Mexico (Bailey, 1931, p. 379), southern Colorado (Warren, 1910, p. 284), southern Kansas (Hibbard, 1934, p. 227), northwestern Oklahoma (Burt, 1945, p. 309), western Texas (Bailey, 1905, p. 214), Baja California (Nelson, 1921, p. 128), Sonora (Burt, 1938, p. 27), Durango (Allen, 1903, p. 612), Nuevo Leon (Davis, 1944, p. 380), and Queretaro (Miller, 1897, p. 45). There are previously unrecorded specimens from Tamaulipas, Mexico, in the University of Michigan Museum of Zoology and it is likely that further collecting will disclose the presence of this genus in a number of other states in northern and central Mexico as well as in southern Idaho.

Within the range of the genus there are two currently recognized species, *Antrozous pallidus* and *A. bunkeri* Hibbard. These two forms are very closely related and likely will prove to be conspecific. So far as known, *A. bunkeri* has been recorded only from the type locality in southern Kansas (Hibbard, 1934) and from one locality in northwestern Oklahoma (Burt, 1945). *Antrozous pallidus,* whose distribution is much more extensive, is represented by four currently recognized geographic races whose ranges are approximately as follows: *pallidus,* southeastern California and northeastern Baja California east to Colorado and Texas and south to south-central Mexico; *cantwelli,* southern British Columbia and eastern Washington south to northeastern California and northwestern Nevada; *pacificus,* northwestern Oregon south to northwestern Baja California; *minor,* central to southern Baja California.

Antrozous pallidus is primarily a species of the Lower and Upper Sonoran life zones. In parts of Oregon and California, however, it ranges well up into the Transition Zone, locally, and to the south, in parts of Mexico occurs in the Arid Tropical Zone. It has an altitudinal

1. The references cited are not necessarily the first published records but, wherever possible, those that give the most complete distributional accounts for each state or province concerned.

range known to extend from –178 feet in Death Valley, California (Grinnell, 1933, p. 94), to at least 6700 feet in the Quinn Canyon Mountains, Nevada (Hall, 1946, p. 166). These altitudinal extremes are both within the range of the race *pallidus*. In central California, however, the writer has records of *Antrozous p. pacificus* from essentially sea level at Inverness, Marin County, to 5000 feet at Long Barn, Tuolumne County.

Habitat

No attempt is made here to give a general description of the habitat of the pallid bat since environmental conditions vary so much throughout different parts of its rather extensive range. To facilitate a better understanding of the requirements of members of this species, however, some of the situations in which they have been observed are described. These include coniferous forests of several different types, nonconiferous woodland, brushy terrain, rocky canyon, open farm land, and desert. Suitable daytime retreats or roosts, of course, are essential for the occurrence of these bats in any region. It is possible that the presence of available fresh water nearby also is necessary.

Fairly conclusive evidence was obtained indicating that pallid bats occur in Richardson Grove State Park, Humboldt County, California. This grove of redwoods *(Sequoia sempervirens)* is close to the Eel River and there is open country nearby where bats of this species might forage at night. A torpid pallid bat was found at an abandoned cabin in a dense redwood forest in Mill Valley, Marin County, California, on January 15, 1950.

At various times in 1948, 1949, and 1950 Mr. M. Woodbridge Williams noted pallid bats in or around his home in Inverness, Marin County. An individual was captured here on November 7, 1948, and another in August, 1950. Much of the forest growth in the vicinity of the Williams' home is native, consisting principally of Bishop pine *(Pinus muricata)*, coast live oak *(Quercus agrifolia)*, tan oak *(Lithocarpus densiflora)*, and madrone *(Arbutus menziesii)*.

On the evening of May 29, 1939, the writer captured a pallid bat at Long Barn, 5000 feet, Tuolumne County, California. This individual flew in through an open window of a cabin situated in a forest composed principally of yellow pine *(Pinus ponderosa)*, white fir *(Abies concolor)*, and incense cedar *(Libocedrus decurrens)*. Bailey (1936, p. 390) records pallid bats associated with yellow pine in southwestern Oregon.

In San Luis Obispo and Kern counties, California, summering colonies of these bats were found either in buildings or in crevices in rock.

One group of ranch buildings inhabited by them was situated near the mouth of a small canyon which opened out onto a flat that was used for raising grain. The vegetation behind the buildings consisted largely of grasses with clumps of *Eriogonum fasciculatum* and *Artemisia californica* scattered about. There were some large cottonwood, pepper, and fig trees growing near the buildings. Permanent water, provided by a spring, was available close by. Mr. Eben McMillan found another colony of pallid bats living in the attic of a garage in the town of Shandon. There were a good many cultivated trees nearby and open grassland within a quarter of a mile.

Figure 3. Rocky outcrops provide numerous roosting sites in the form of crevices for pallid bats. Photographed near Carneros Spring, Kern County, California, May 20, 1948, by G Dallas Hanna.

Five colonies were found in natural rock crevices. Two of these colonies were located within several hundred yards of each other in a large outcrop of sandstone at the northwestern edge of the Carrizo Plain, San Luis Obispo County. Some of the rocks were 50 to 60 feet in height. Immediately surrounding the outcrop was grassland intermingled with a good many trees and shrubs including blue oak *(Quercus douglasii)*, islay *(Prunus ilicifolia)*, great-berried manzanita *(Arcto-*

staphylos glauca), black sage *(Salvia mellifera),* California sagebrush *(Artemisia californica),* and *Aplopappus cuneatus.* During the dry season the nearest available water was about one-half mile distant. Another colony was found in a sandstone outcrop 2½ miles northwest of Carneros Spring, Kern County. The surrounding terrain was extremely arid (fig. 3). A few low-growing shrubs, principally California sagebrush and *Eriogonum* sp., were present near the base of the rocks. Whether or not there was any water available to bats nearer than Carneros Spring was not determined. Two other colonies were found inhabiting rocky escarpments bordering a small valley through which San Juan Creek flows, 3 miles southeast of La Panza, San Luis Obispo County (fig. 4). The valley was no more than one-quarter of a mile in width. A few oaks were scattered about in the grassland and an occasional willow grew along the streamside.

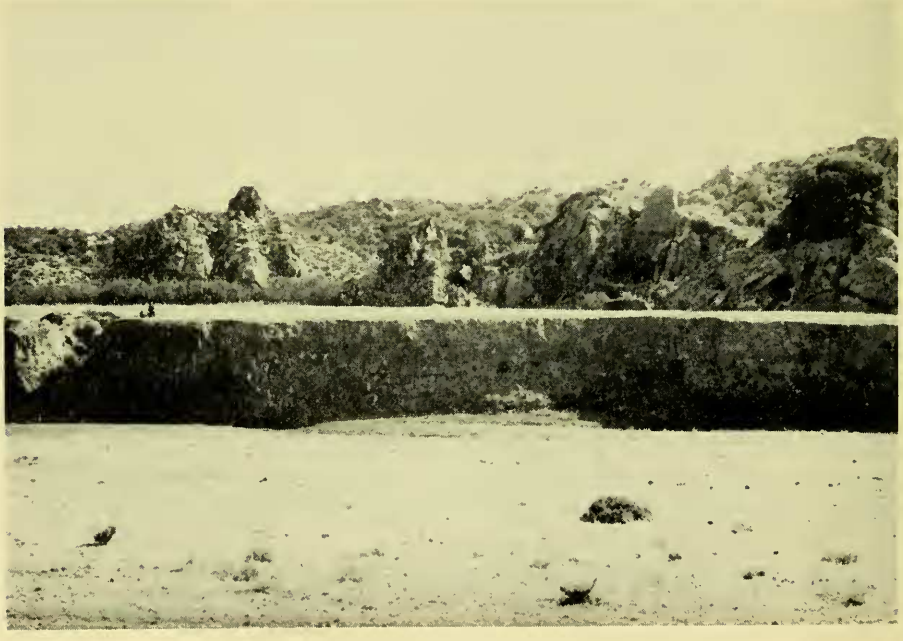


Figure 4. Favorable habitat for pallid bats on the La Panza Ranch along San Juan Creek, San Luis Obispo County, California. Photographed June 9, 1948.

A number of other chiropteran species were observed in the general area inhabited by the pallid bats in San Luis Obispo and Kern counties. These included *Myotis yumanensis, M. thysanodes, M. volans, M. californicus, M. subulatus, Pipistrellus hesperus, Eptesicus fuscus, Corynorhinus rafinesquei, Tadarida mexicana,* and *Molossus perotis.*

Hall (1946, p. 163) comments that in the Carson Basin, Churchill County, Nevada, the pallid bat "frequents the edges of the basin, foraging there as well as roosting in the caves along the outcrops of rock at the foot of the hills." Burt (1934, p. 397) records this species as a common inhabitant of the lower desert regions of southern Nevada, especially around ranch houses where water and vegetation are present.

Roosts

During most of the spring, summer, and autumn months pallid bats are found during the daylight hours in groups or colonies generally consisting of no more than one hundred individuals and frequently composed of a considerably smaller number. The cavities or crevices which provide daytime roosts for these colonies may be in rocks, trees, or various man-made structures as has already been indicated. Irrespective of their diversity in location, all of the roosting places examined appeared to have certain features in common. All provided semidarkness, and protection from above. The ventral surface of the body of a roosting bat was always against a solid surface which was either a part of the roost or the body of another bat. Roosting pallid bats were never observed hanging freely from a horizontal surface, such as the roof of a cave, in the daytime. Some other species of bats regularly hang in this latter manner. The opening from the roosting crevice to the outside was, with one exception, at least several feet, usually much more, above the substratum, thus permitting the bats both to take flight immediately after emerging and to fly directly into the opening when returning. The opening was generally beneath the roost although when the roost was in a building it was frequently necessary for the entrance to be on a horizontal plane.

In the event that pallid bats are disturbed at their roost they frequently will leave and go to an alternative roost which is usually located nearby. The permanence of such moves is not known. In at least two instances roosts that were so vacated, as a result of disturbance, were found unoccupied during the succeeding several years. There is some indication that the shifting of a colony from one site to another is sometimes done without apparent provocation. On several occasions roosts were found to be inhabited in the spring and were left undisturbed by the observer. When examined several months later they were unoccupied. Although it is possible that these colonies were disturbed by someone in the meantime, their locations were such as to make this exceedingly improbable. Ryberg (1947, pp. 74–77) comments on similar alternative roosts used by certain species of bats in northern Europe, and Pearson, Koford, and Pearson (1952, p. 276) com-

ment on the alternative roosts of summering colonies of *Corynorhinus*.

Since pallid bats are not primarily forest dwellers, roosts in cavities in trees are of relatively uncommon occurrence. On August 9 and 10, 1947, Mary Louise Perry (MS) visited Richardson Grove State Park, Humboldt County, California, in search of pallid bats reportedly inhabiting hollow redwood trees in the grove. A number of hollow trees were examined and two were found to have been inhabited by bats although no bats were observed at this time. In the base of one tree the guano indicated that the inhabitants were probably all *Myotis*. About 98 per cent of the droppings in the other appeared to be those of *Myotis* but the remainder were large, about the size of those of *Antrozous*. According to Mr. Earl P. Hanson, assistant district superintendent at Humboldt Redwood State Park, *Antrozous pallidus* and *Myotis californicus* were the only species of bats that had, up to that time, been identified from Richardson Grove. Bailey (1936, p. 390) records a colony found in a hollow yellow pine in Jackson County, Oregon. The same author (1931, pp. 379–380) mentions another instance in which pallid bats that were disturbed in a cave in the daytime were noted seeking refuge in a hollow tree in the Cloverdale Hills in southwestern New Mexico. Hall (1946, p. 163) records a small group of these bats found roosting in a hole in a cottonwood tree at Ash Meadows, Nevada. Davis (1944, p. 380) found a colony of pallid bats using a cavity in a dead cypress as a daytime retreat in Nuevo Leon, Mexico.

While cavities in trees occasionally provide natural daytime retreats, crevices in rocks are most frequently used for this purpose. Several such daytime retreats were observed in San Luis Obispo and Kern counties. One of these was found on May 10, 1947, beneath a partly loosened slab of rock on a perpendicular cliff of an isolated sandstone outcrop 2½ miles northwest of Carneros Spring, Kern County (fig. 5). The entrance to the crevice was 7 feet above the ground and measured 2 feet in length and 4 inches in width. The crevice extended upward between the slab and the cliff for about 3 feet. The bats were crowded into the upper part of the cavity. The cliff below the opening was stained with urine and excrement and the ground beneath was covered with guano. Disturbance caused the bats to leave and fly around to another side of the outcrop where they were thought to have taken refuge in another crevice about 75 feet above the ground. The distance between these two crevices was about 100 yards. The roost which the bats had left was found unoccupied on September 20, 1947, although numerous droppings in the vicinity indicated that a colony of pallid bats still inhabited this isolated outcrop.

On June 7, 1948, two more colonies were located beneath loose slabs

Figure 5. The crevice beneath the loose slab of sandstone in the center of the picture served as a day roost for a colony of pallid bats. Two and a half miles northwest of Carneros Spring, Kern County, California, September 20, 1947.

of sandstone at a rocky outcrop on the northwestern edge of the Carrizo Plain in San Luis Obispo County. One of the colonies occupied a daytime roost very similar to that just described. In this instance the entrance to the crevice was 12 feet above the ground. The colony was not disturbed on this date. On October 23, 1949, pallid bats were again found in this crevice and in a similar crevice 30 feet away. The entrance to the latter was only 6 feet above the ground. These two roosts were considered as belonging to the same colony. The second colony found on June 7, 1948, was about 200 yards from the one just described. The retreat occupied by these bats was also behind a partly loosened slab of sandstone on a cliff but it was situated about 20 feet above the ground and just above a narrow ledge of rock that was sufficiently wide for a person to walk on. The main entrance to the roost was a narrow, vertical opening, about 12 inches in length and 2 inches in width, at one side of the slab. The bottom of the opening was 12 inches above the ledge. Along the lower edge of the slab, where it contacted the ledge, there were two holes about a foot apart. Each hole measured approximately 3 inches in diameter. Accumulations of excrement that had rolled out through the holes were present on the ledge. All of the bats in this colony were crowded tightly together at the upper end of the crevice which was about 18 inches above the ledge. This was the only roost observed where the bats were unable to drop immediately after emerging. The ledge prevented them from so doing. Approximately two-thirds of the occupants were captured as they attempted to come out. The rest escaped. Those that escaped appeared to have no difficulty in taking flight immediately upon coming out of either the vertical slit or the two holes. The captured bats were released a short time later, after their sex had been recorded and the females palpated to determine pregnancy. The majority of those that either escaped or were released flew to a crevice in the roof of a shallow cave about 50 yards away. This alternative roost was known to have housed a colony of pallid bats the previous summer. When these roosts were visited on October 23, 1949, both were found uninhabited. It was difficult to tell whether the alternative roost in the roof of the cave had been used in the daytime during the summer of 1949. There were large accumulations of guano belonging to both pallid bats and Mexican free-tailed bats but both species were known to use the roof of this cave regularly as a night roost during the summer. The roost above the ledge showed no sign of having been occupied in 1949. When it was visited again on April 14, 1951, it was found to be occupied by a wood rat *(Neotoma lepida)*. This suggests the possibility that wood rats occasionally compete with these bats for home sites.

On June 8, 1948, two other colonies of pallid bats were found on the La Panza Ranch along San Juan Creek, San Luis Obispo County, about 9 miles west of Simmler. One was located in a crevice beneath a loose slab of rock on the face of a nearly vertical cliff (fig. 6). The entrance to the crevice was 10 feet above the ground and consisted of an opening 3 feet in length and about 4 inches in width. The crevice extended upward approximately 3 feet and the bats were in the uppermost part. When some of these bats were captured the following day the other members of the colony left. All those seen leaving flew down the canyon through which the creek flowed and were out of sight as soon as they rounded a bend several hundred feet away. One gained the impression that they were moving to an alternative roost known to them although this was not found by the observers. The roost deserted at this time was found occupied in the summer of 1949 and again in the spring of 1951. It was not examined in 1950.

The second colony found on June 8, 1948, on the La Panza Ranch was about half a mile farther up the canyon in a small cave. The cave, situated at the base of a sandstone cliff, was dome-shaped and about 10 feet in diameter. The distance from the floor of the cave to the highest point was also about 10 feet. On one side of the dome there was a funnel-shaped recess which led into a short, narrow crevice in which the bats were observed roosting. There were two openings into the cave from the outside. One of these was irregular in shape. It extended from the ground up to a height of 3½ feet and was about 2½ feet in width. Above this, about 5 feet from the ground, there was another opening 1 foot wide and 2 feet in height. The lower opening, judging from the presence of many droppings, was the one more frequently used by the bats when entering or leaving. In the center of the floor of the cave there was a broad, cone-shaped pile of excrement 3 to 4 feet in diameter and attaining a maximum depth of 12 inches. The presence of observers close to this cave during the night caused the colony to move to another roost by dawn the following morning. It was visited in the summer of 1949 and again in the spring of 1951 and found unoccupied in the daytime on each occasion although fresh accumulations of guano in each instance showed that the dome of the cave still served as a night roost.

There is a possibility that these bats might roost beneath rock slides or in talus slopes in certain localities although no such colonies have been located. Racey (1933, p. 18), however, records the discovery of a single bat of this species beneath a pile of stones in British Columbia.

Pallid bats frequently find suitable roosts in atties, between walls, between bridge timbers, and in other similar hiding places in man-made structures. One such colony that was periodically under obser-

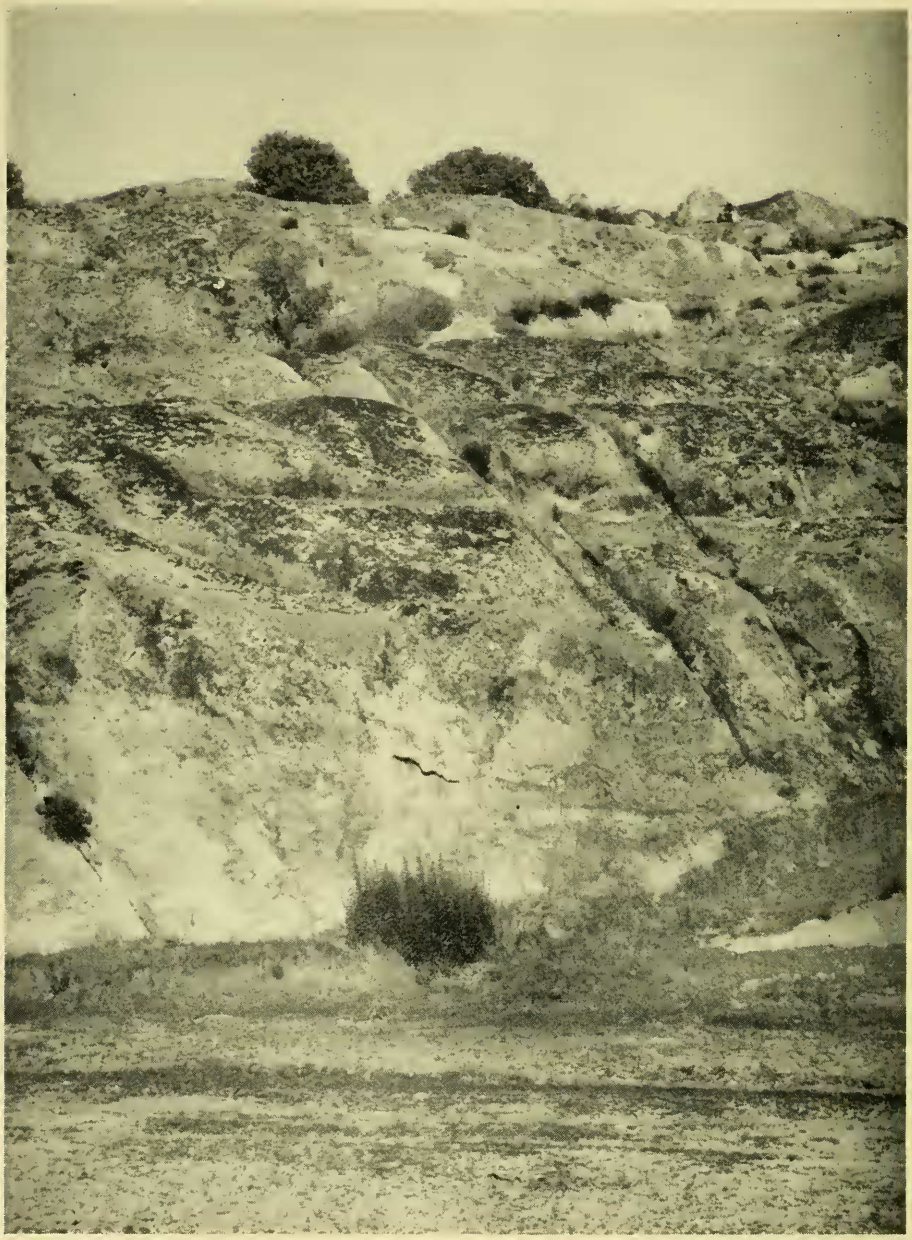


Figure 6. The crevice on the sandstone cliff in the center of the picture housed a colony of pallid bats. La Panza Ranch, San Juan Creek, San Luis Obispo County, California, June 9, 1948.

vation during this study inhabited a barn (fig. 7) and a shed immediately adjacent to the barn on a ranch 4½ miles northeast of Shandon, San Luis Obispo County. Sometimes the entire colony was in one or the other of the buildings and sometimes it was divided, with bats in both buildings. In each structure the bats occupied small spaces at either end between the timbers that supported the roof. Since the crevices were small and could not hold many bats, the colony was divided into a number of groups. Disturbance never caused members

Figure 7. Pallid bats inhabiting this barn, 4½ miles northeast of Shandon, San Luis Obispo County, California, were observed entering and leaving through the opening seen immediately below the peak of the roof. Photographed October 22, 1949.

of this colony to desert the buildings although they might fly from one building to the other or move to the opposite end of the roof of the same building.

On June 7, 1951, Sterling Bunnell examined a colony of pallid bats living in the attic of Encina Hall at Stanford University in Palo Alto. Some adult females and young were captured. The writer examined the attic of this building a few days later on June 13. The attic was found to be divided into a number of sections, each about 40 feet long and equally wide. Brick walls served as partitions between adjoining sections. Beams 2 inches by 12 inches rested on the brick partitions and supported the roof. No bats were found in the section where they had been roosting on June 7 although there were large accumula-

tions of droppings at the bases of the brick partitions at each end. Two partitions away, however, about 40 pallid bats were found roosting in spaces between the top of one of the brick partitions and the roof. It seemed likely that these were the same bats that had been living in the other part of the attic on June 7.

Another colony discovered by Eben McMillan (*fide* letter of April 24, 1949) in western San Luis Obispo County, between Paso Robles and Cambria, was located in a space between the window panes and some boards that had been nailed across the windows of an old house.

There are numerous records in the literature of pallid bats using man-made structures, a few of which are cited here. Krutzsch (1946, p. 241) records bats of this species living in a barn, in the attic of a church, and in cracks between the beams of a bridge. Hall (1946, p. 163) describes a group of these bats found near Lahontan Dam, Nevada, that had "ensconced themselves in the crevices, ½ to 1 inch in width, between the 18-inch timbers on the underside of a bridge." Storer (1931, p. 244) records a summering colony of pallid bats found living in the walls of a residence in Berkeley, California. Bailey (1905, p. 214) mentions pallid bats roosting behind a signboard at Comstock, Texas.

At night pallid bats frequently alight, at what are generally referred to as night roosts, to rest or to consume food that has just been captured. These so-called night roosts are much more accessible to the bats than the crowded recesses that constitute daytime retreats. Bats living in barns or attics usually use the ridgepole of the roof for such purposes. In rocky areas the roofs of shallow caves frequently provide night roosts (fig. 8). Large accumulations of guano and parts of insects that have been discarded are present beneath such roosts (fig. 9). Early in April, 1949, the floor of one such roost in a small cave on the La Panza Ranch was scraped clean. When examined six months later on October 23 a new accumulation of guano was found that measured 4 feet in diameter and 7 inches in depth in the center.

The night roosts of all the colonies whose daytime retreats were known were usually within a few yards of these daytime retreats. In one instance the night roost of a colony was not located although no great effort was made to find it in the numerous rocky recesses nearby. Several night roosts regularly used by pallid bats were found although diligent search failed to reveal the whereabouts of the day roosts. In each instance, however, possible hiding places nearby were inaccessible to the observer.

The night roosts of these bats in buildings are frequently a source of considerable annoyance to the owners. Bats belonging to one colony under observation used, for this purpose, either the ridgepole of a barn or the ridgepole of an adjacent shed that served as a garage. As a re-

Figure 8. The roof of this shallow cavern near San Juan Creek on the La Panza Ranch, San Luis Obispo County, California, served as a night roost for pallid bats and Mexican free-tailed bats. Photographed June 8, 1948.

Figure 9. Accumulation of guano beneath the night roost shown in figure 8. Photographed October 23, 1949.

sult, the bat excrement fouled hay that was stored in the barn and made it necessary to hang a cloth covering over the car in the garage to keep it clean. Members of another colony were observed using the beams supporting the roof of an open porch of a ranch house for a night roost. The house was less than one year old when examined on the evening of April 13, 1951, and the two-by-four beams of the porch roof had been freshly creosoted. This apparently was no deterrent as 6 bats were seen hanging from a beam at one end of the porch and 3 from a beam at the opposite end at 9:55 P.M. Fresh droppings and insect remains were found on the concrete beneath each small group.

The fact that an electric light had been burning on the porch all evening did not seem to discourage the bats from coming here any more than did the creosote.

SEASONAL BEHAVIOR

Spring and summer: By late March or early April the period of dormancy appears to terminate in central California and summer colony formation occurs. Mrs. Grinnell (1918, p. 356) records March 27 as the earliest known date of observation of this species in spring in this state. In Texas, Bailey (1905, p. 214) indicates April 18 as the earliest seasonal date on which the species was noted.

In the spring of 1949 an examination of four sandstone crevices in eastern San Luis Obispo County, where summering colonies had been observed in 1947 and 1948, failed to reveal the presence of any pallid bats on April 1, 2, and 3. A very few fresh droppings beneath two of the colony sites indicated that one or at most a very few bats had recently been present. During the ensuing two weeks Mr. Eben McMillan periodically visited one of these colony sites and a barn in which pallid bats had been found every summer for some years. Bats were found in the barn on April 10 and in the sandstone crevice on April 14. In each instance they appeared to have arrived not more than a day or so previously. No effort was made to determine the number of individuals present on the first day bats were found in these colonies, but on April 15 it was estimated that about 30 individuals were present in the colony first occupied on April 10. Seventeen of these were captured, of which 15 were females and 2 were males. Five of the females were banded bats that had been captured by the writer at the same place on September 20, 1947, and kept in captivity in San Francisco until June 6, 1948, at which time they were released at the original site of capture. This represented a 25 per cent return since 15 other pallid bats, taken at the same place and on the same date, were also released here with bands on their forearms on June 6, 1948. It is probable that additional banded individuals were present in the colony on April 15, 1949, but they were not captured.

This same colony was visited on April 14, 1951. The owner of the ranch on which the barn that housed the bats was situated stated that the colony had made its appearance several weeks before. Difficulty in gaining access to the roof of the barn made it possible to capture only 5 females and 4 males, although many more bats were heard and known to be present. Two of the females and one of the males were banded bats. One female belonged to the group originally captured on September 20, 1947, and released on June 6, 1948, after being kept

in San Francisco for some months. It was not one of those recaptured on April 15, 1949. The other female and the male had been banded at this colony on October 22, 1949, and released immediately. On March 20, 1953, Dr. and Mrs. Karl B. Koford visited this colony and found 4 females and 1 male present. An unusually mild winter and early spring may have accounted for the early seasonal appearance of bats at this summer colony in 1953.

A second roost, known to have been inhabited the previous three summers, was visited on April 14, 1951, and found to be occupied. The small quantity of fresh guano on the previous years' deposit beneath the roost indicated that the colony had not been established here more than a week or two. Although about 40 pallid bats were estimated to be present, only 11 were captured. Two were males and 9 were females. In addition, 7 Mexican free-tailed bats were taken (2 males, 5 females). All were weighed, examined for parasites, and then released.

So far as known pallid bats are gregarious during the spring and summer months. The number of adult individuals comprising a colony was found to vary from about 30 to approximately 100. There is considerable variation in the sex ratio in different colonies and, seemingly, even within the same colony at different times. Luther Little (Mailliard, MS) captured 19 adults from a fairly large colony inhabiting a deserted building in Lake County, California, on April 16, 1919. Eighteen were males and 1 was a female. Twenty-two adults captured at random from a colony composed of about 40 individuals inhabiting the attic of Encina Hall, Stanford University, California, on June 13, 1951, consisted of 15 males and 7 females with young. Five adult females, however, had been taken from this same colony by another person the week before. Of 15 adults captured in western Kern County on May 10, 1947, from a colony estimated to consist of about 100 individuals, 8 were males and 7 were females (either pregnant or with young attached). Three adult males and 4 females, pregnant or with newborn young, were secured from a colony of 60 bats in eastern San Luis Obispo County on June 9, 1948. Two days previously a random sample from another colony of similar size several miles away consisted of 7 adult males and 35 pregnant females. Thirty-seven pallid bats captured from another colony in this region on September 20, 1947, consisted of 8 males and 29 females. At this time the number of individuals in the colony was estimated to be somewhat in excess of 60. On June 6, 1948, 26 adults were captured at random at this same colony. Sixteen were males and 10 were pregnant females. As has been previously stated, on April 14, 1949, shortly after the formation of this colony in the spring, a random catch produced 2 adult males and 15 adult females. Another random catch on April 14, 1951, produced 4

adult males and 5 adult females, and on March 20, 1953, there were 1 adult male and 4 adult females in the colony.

Storer (1931, p. 244) records the capture of 8 adult or nearly adult males and 13 females, either pregnant or with young, from a colony of pallid bats living between the walls of a residence in Berkeley, California, on June 24, 1919. Hall (1946, p. 163), on the other hand, referring to this species in Nevada, states that "Pallid bats separate by sex in spring before the young are born. The females then are in colonies. About fifty females is the largest number observed in one colony." Dalquest (1947, p. 24) records a colony of pallid bats, consisting of about 60 males, found in the attic of an old winery near Angwin, Napa County, California, on July 8, 1945.

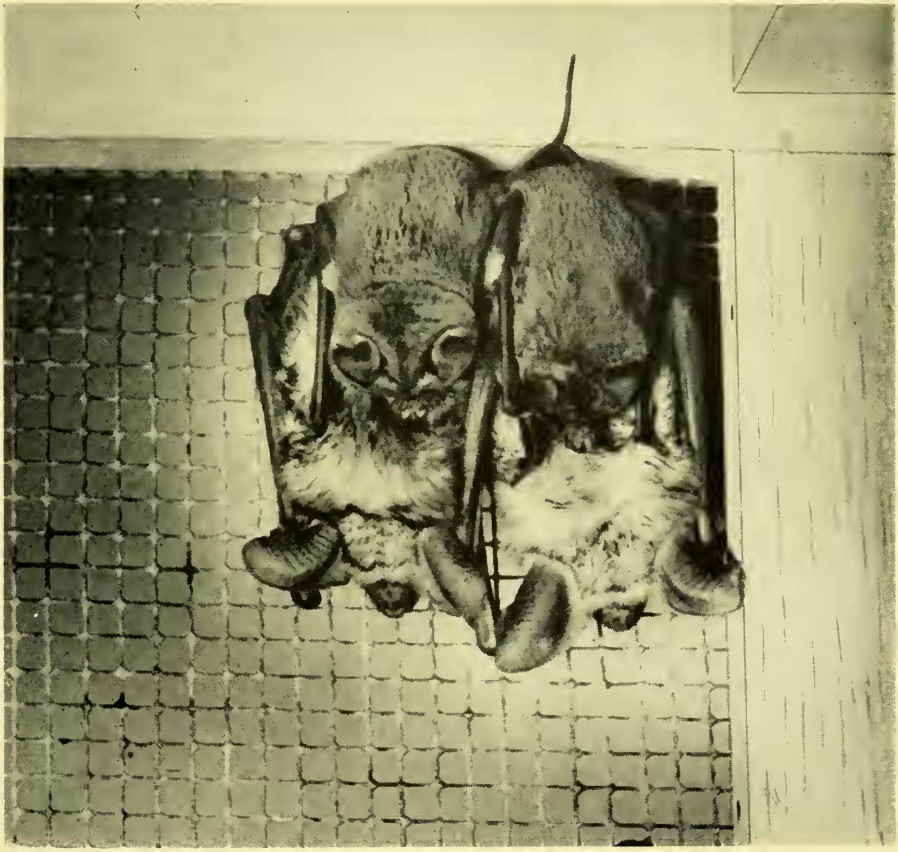


Figure 10. Mexican free-tailed bats are very frequently associated with pallid bats in the wild. When housed in the same laboratory cage members of the two species stayed together. Photographed at the California Academy of Sciences, December 12, 1952.

From the foregoing observations it can be seen that, in California at least, summering colonies may be composed of adults of both sexes and that either sex may predominate in numbers.

Although big brown bats *(Eptesicus fuscus),* several species of *Myotis,* and lump-nosed bats *(Corynorhinus rafinesquei)* may occasionally be found in the same cave, building, or even attic with pallid bats in the daytime during the summer, they do not seem to share the same roost with members of the last species. Only the Mexican free-tailed bat *(Tadarida mexicana)* is commonly found in pallid bat roosts (fig. 10). Most of the pallid bat colonies examined were found to contain one or more of these small molossids. The greatest number observed with pallid bats in one colony was 17. Members of either or both sexes may be represented, including pregnant females in the late spring and summer. Individuals of this species were found to be equally common in colonies of big brown bats.

Krutzsch (1946, p. 241), discussing big brown bats in San Diego County, California, states that: "*Eptesicus, Tadarida,* and *Antrozous* have been found living successfully in the same building, a barn on the grounds of The Old People's Home, in the attic of the San Marco Church, and in various cracks between the "I" beams of the bridge at the juncture of Highways 79 and 80." Dalquest (1947) mentions finding *Corynorhinus rafinesquei, Myotis yumanensis, Myotis thysanodes,* and *Tadarida mexicana* inhabiting the same buildings as pallid bats during the daytime. Bailey (1936, p. 392) records a mixed colony of pallid bats and Mexican free-tailed bats found in Carson Valley, Nevada. Hall (1946, p. 165) records 2 pipistrelles *(Pipistrellus hesperus)* and 1 little brown bat *(Myotis californicus)* hanging in a mine tunnel in which 2 pallid bats were found hibernating near Yerington, Nevada, on December 27, 1939.

Fall: By the middle of September the adults have all completed the annual molt (many have done so by the middle of summer) and the young of the year have matured to the stage where they are indistinguishable, at least in the field, from adults. No evidence was obtained to indicate dissolution of the summer colonies this early. By the middle of October, however, the summer colonies tend to break up into smaller groups. At this time pallid bats may be found in situations where they do not occur in summer.

On October 22 and 23, 1949, some known summer colony sites in eastern San Luis Obispo County were examined. The first colony visited was in the barn, previously mentioned, where 20 banded individuals captured on September 20, 1947, had been released on June 6, 1948. Although over 60 bats were generally found here in summer there were only 12 on October 22. Six were males and 6 were females.

One of the females was a banded individual, one of the group captured on September 20, 1947.

Examination of a deserted cabin about one mile from this colony resulted in the discovery of a male and a female pallid bat hanging side by side behind a loose board in one of the rooms. Although this cabin had been investigated many times before in winter, spring, and summer, the only bats previously found here had been of the species *Myotis subulatus*. Later that evening the night roost of another colony of pallid bats was visited and 8 or 10 individuals were observed hanging there before the approach of intruders disturbed them.

The following day the site of another summer colony was visited. It contained only 7 bats, 5 of which were captured. Two of these were males and 3 were females. About 30 feet away another small group composed of 13 pallid bats was discovered. Only two of these were captured. They proved to be females. Examination of two other summer colony sites that day showed that one had recently been vacated while the other contained 5 pallid bats and 15 Mexican free-tailed bats. None of the former were captured.

Mr. Eben McMillan made some interesting observations on the appearance of pallid bats in the fall of 1948 and 1949 on the Pinole Ranch at the north end of the Carrizo Plain in eastern San Luis Obispo County. No pallid bats were seen about the ranch buildings in the spring or summer months of these two years. In 1948, however, between the latter part of October and the middle of November, pallid bats were found hanging each night from beams supporting the grain bins. Each morning during this period numerous droppings and fragments of insects, presumably discarded by the bats, were found on the ground beneath the beams. After the middle of November the bats were no longer seen. In 1949 pallid bats again appeared here during the second week in October. On October 23 the writer observed many fresh droppings as well as remains of Jerusalem crickets on some clean sacks that had been placed beneath this temporary night roost the evening before. During the next week or so Mr. McMillan examined the sacks each day and then cleaned them. After October 25 there was a gradual decrease in the number of droppings found daily until November 1. On this date there were only two droppings and none were found subsequently that year.

Winter: Very little information is available regarding the whereabouts of pallid bats between the middle of November and the end of March. They are not to be found in their summer retreats nor are they active at night, as far as could be determined. There is no evidence to indicate that members of this species migrate in the strict sense of the word although unquestionably there is a local shifting

and probably a dispersal of summer populations. Such meager information as was acquired seems to indicate that single individuals or small groups of these bats seek remote retreats where they are not likely to be disturbed.

Referring to this species in Nevada, Hall (1946, p. 165) says: "The hibernating individuals consisted of two males found December 27, 1939, in a mine tunnel 9 miles east and 2 miles north of Yerington, 120 and 138 feet from the mouth of the tunnel. Each bat was in a crevice in the roof of the tunnel and had its ears erect and its eyes open. The bats were unable to fly and their movements were slow. The temperature inside the mine where the bats were was 60°F.; outside the mine it was between 40° and 50°F. (Alcorn, MS)." Alcorn (1944, pp. 309–310), referring to the same cave, mentions that pallid bats were noted here during three winters.

Mrs. Grinnell (1918, p. 356) records two females in the collection of Stanford University taken on January 1, 1895, at Carmel Mission, Monterey County, California. A female (no. 106583) in the collection of the Museum of Vertebrate Zoology, University of California, was taken at Woodside, Santa Clara County, on January 17, 1947. It weighed 22.3 grams.

On January 18, 1950, a male pallid bat was received that had been captured three days previously in Mill Valley, Marin County, California, by Thomas Leech. Although the animal had been in captivity for three days its weight upon receipt was 26.5 grams. A few days later, January 22, the writer visited the place where the bat had been found. It proved to be an old, deserted, one and one-half story cabin situated in a rather dense redwood forest on a northeast-facing slope. The bat had been found hanging on the outside of the building beneath an old piece of damp canvas where it undoubtedly was dark, cool, and damp all winter. Further search failed to uncover any additional pallid bats, although a female big brown bat *(Eptesicus fuscus)* and a female lump-nosed bat *(Corynorhinus rafinesquei)*, each dormant, were hanging within the cabin.

On December 1, 1940, E. Raymond Hall, Ned Stone, and Thane Riney found a male and two female pallid bats in a crevice in a limestone cliff 6 miles east of Walnut Creek, 1450 feet, Contra Costa County, California. The surrounding territory was covered with chaparral (Perry, MS).

Dr. Charles G. Sibley informed the writer that on January 28, 1940, he found 4 pallid bats in a semitorpid condition inside a hollow post holding up one end of an old lean-to on Bolinas Ridge, 1500 feet, Marin County, California. His attention was directed to the presence of the bats by faint noises, reminiscent of small mice, coming from within

the post. Two of the bats were males, weighing 25.8 and 28.5 grams, and 2 were females, weighing 28.3 and 32.5 grams. They are now in the collection of the Museum of Vertebrate Zoology (nos. 90572–90575).

On March 13, 1950, Mr. Eben McMillan found a torpid female pallid bat hanging beneath a loose board in a deserted cabin about 5 miles northeast of Shandon, 1300 feet, San Luis Obispo County, California. This is the only possible winter record that was obtained from San Luis Obispo and Kern counties. Mr. McMillan and the writer had found a male and female of this species, in breeding condition, hanging beneath this same board on October 22, 1949. Careful search for wintering bats, on other occasions, in old buildings, mine tunnels, caves, and other possible retreats in parts of Monterey, San Luis Obispo, and Kern counties failed to reveal the presence of any pallid bats although bats of the following species were located: *Myotis thysanodes, Myotis volans, Myotis subulatus, Eptesicus fuscus,* and *Corynorhinus rafinesquei.* In this region, however, there are countless natural crevices in cliffs and rocky outcrops that are essentially inaccessible for human examination and which could serve as adequate hiding places for wintering bats.

Effect of enforced dormancy: Efforts were made to determine the effect of a simulated winter environment on captive individuals. On September 25, 1947, 6 females and 2 males, that had been captured a few days previously in eastern San Luis Obispo County, were placed in a small retaining cage in a refrigerated room where the temperature ranged from 40°F. to 50°F. To maintain fairly high humidity within the cage the screened front was covered with burlap which was dampened daily. A container with water was kept on the floor of the cage. No food was given the animals during the ensuing weeks.

The 2 males died, one after 14 days and the other at 40 days. Two of the females also died, one at 8 days and the other at 36 days. The death of some of these bats was suspected to have resulted from the toxic effect of aniline dyes placed on their bodies as a means of identification. The remaining 4 females were removed to a warm laboratory at the end of 43 days. During this period of enforced dormancy they had been weighed weekly. Occasional increases in weight were attributed to water that was believed to have been taken from time to time. The average loss in weight, per bat, at the end of 43 days amounted to 8.1 per cent or 0.184 per cent per day. The gradual loss in weight of 2 of these bats is shown in figure 11.

During the 28 days following the period of enforced dormancy these two bats were kept in a small cage in the laboratory and fed daily. Daily records were kept of their weights. As is shown in figure 11 there was a very rapid increase in weight during this time. The average increase, per bat, at the end of 27 days amounted to 60.8 per cent or 2.25

per cent per day. On the last day there was a slight decline in the weight of each bat.

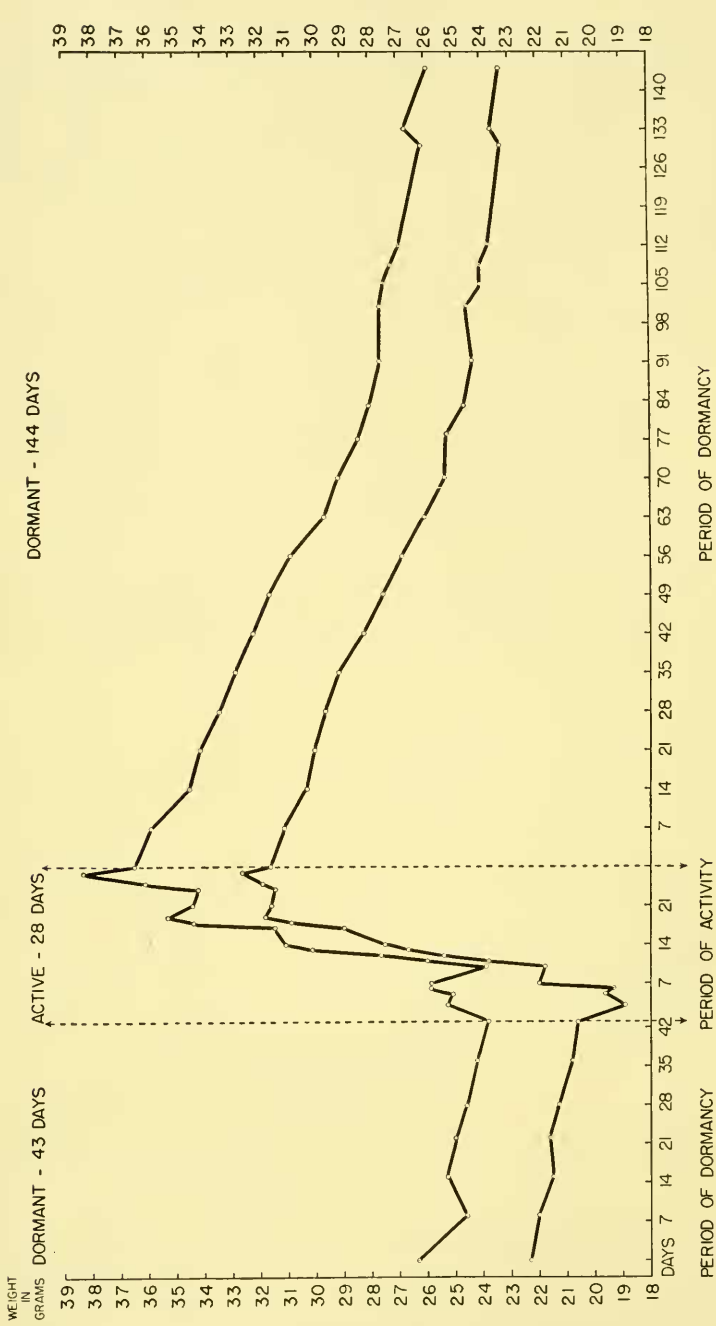
At the end of this 28-day period these two bats were returned to the refrigerated room and kept there from December 5, 1947, until April 27, 1948, under the same conditions used in the first dormancy experiment. At the end of this period of 144 days the decline in body weight, per bat, averaged 27.6 per cent or 0.193 per cent per day (fig. 11).

On November 15, 1950, 4 pallid bats (3 males, 1 female) that had been captured at Farmington, San Joaquin County, California, on October 27, 1950, were placed in a cage in a refrigerated room and kept there until March 14, 1951. They were provided with drinking water and the front of the cage was kept covered with damp burlap. During this period of 119 days the temperature of the room was kept at 38°F. to 40°F. The bats were weighed weekly. The average loss in weight, per bat, amounted to 24.96 per cent or 0.209 per cent per day (fig. 12).

In each of the three dormancy experiments mentioned the bats hung from the screened side of the cage. The water container was visited by one or more of the bats about every 3 to 5 days. This was demonstrated by placing a thin layer of fine dry sand on the bottom of the cage and examining it every day or so for tracks. When tracks were found leading to the water dish the sand was smoothed over again. Several investigators have previously suggested the possibility that hibernating bats are periodically aroused by thirst. This may have been true of these captive individuals since they periodically visited the water container and on several occasions a temporary increase in body weight was noted. Under natural conditions most hibernating bats that have been studied are not far from water, either in the form of accumulated droplets in the hibernacula or in streams and ponds nearby. Folk (1940, p. 312) observed little brown bats *(Myotis lucifugus),* aroused from a torpid condition in winter in a cave in New York, lapping drops of moisture condensed on the wall. Furthermore, there is occasional shifting of individuals during the general period of dormancy which may be the result of movement to and from water. As is shown in figures 11 and 12 the greatest loss in weight occurred during either the first or second week of enforced dormancy.

The respiration rate in dormant individuals varied greatly and

Figure 11. Graph showing changes in body weights of 2 pallid bats kept without food at 40°F. to 50°F. for 43 days, then removed to a warm laboratory room and fed for 28 days, following which they were again kept at 40°F. to 50°F. without food for 144 days.


WEIGHT IN GRAMS
DORMANT - 43 DAYS
ACTIVE - 28 DAYS
DORMANT - 144 DAYS
DAYS
PERIOD OF DORMANCY
PERIOD OF ACTIVITY
PERIOD OF DORMANCY

was difficult to determine accurately. Bats cannot be said to become truly torpid since even the turning on of a light in the refrigerated room at times stimulated breathing. The noise involved in the opening of a door or the sound of footsteps had the same effect. Numerous respiratory counts made on the bats maintained in a refrigerated room showed a range of 0 to 52 per minute. The greatest period in which no obvious sign of breathing was observed was 4 minutes.

Dormant bats, when suddenly handled, reacted feebly at first. The mouth was generally opened wide and a weak buzzing sound produced. Following this, if the wings were free, one or both of them would be slowly extended and then held stiffly in an outspread position. No attempt, of course, was made to disturb dormant individuals any more than was necessary. When two females were placed in the sun in an outdoor flight cage after 144 days of confinement without food in a refrigerated room they were capable of sustained flight within 15 minutes.

Neither bats kept in the laboratory nor those in outdoor flight cages became dormant for any considerable period of time during the winter. They were, however, more sluggish and ate less at this season. Those in outdoor cages occasionally failed to take any food on cold or stormy nights.

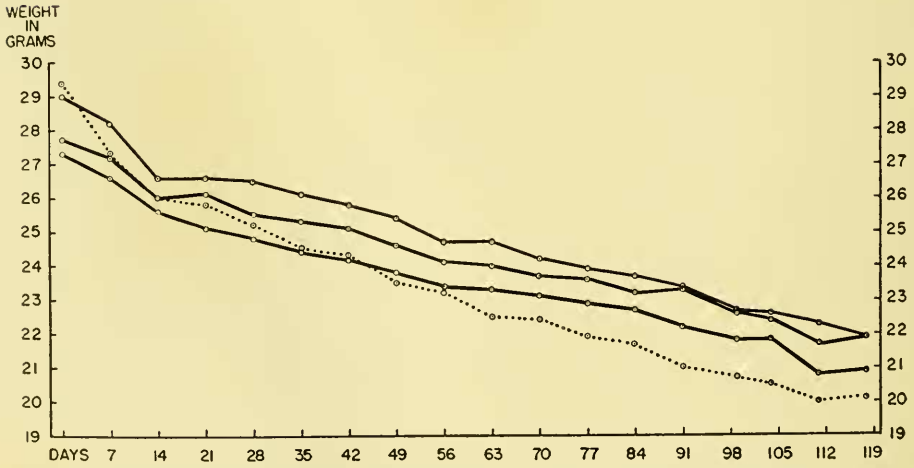


Figure 12. Graph showing gradual loss in body weights of 4 pallid bats kept at 38°F. to 40°F., without food, for 119 days. Solid lines indicate males, the dotted line a female.

Seasonal fluctuation in body weight: As is shown in figure 11, captive pallid bats are capable of increasing body weight rapidly after a period of dormancy. Data on bats from a single colony, presented in table II, indicate that this is also probably true of these bats in the wild. Males captured in April, 1951, several weeks after their appearance in the summer colony, weighed about the same as males taken in June. Males captured only a few days after their arrival in the summer colony in April, 1949, weighed considerably less. Females continued to increase in weight from the time of their arrival in spring until the young were born. Although no opportunity was afforded to secure weights of females from this particular colony immediately after the period of parturition, the average and extreme weights of 7 females, captured June 13, 1951, in Santa Clara County, California, that had young from about 3 to 6 weeks old, were 26.8 (25.1–29.3) grams. There appeared to be an increase in the weight of bats of both sexes again in the fall.

TABLE II

Average weights, in grams, of pallid bats from a single colony 4½ miles northeast of Shandon, San Luis Obispo County, California, in spring, summer, and autumn. Figures in parentheses represent numbers averaged.

Date	Males	Females	Reproductive Status
April 16, 1949	20.6 (2)	24.3 (15)	Females had recently ovulated
April 14, 1951[2]	25.1 (3)	31.7 (2)	Females with well developed embryos
June 6, 1948	25.2 (16)	34.7 (10)	Females in late pregnancy
October 22, 1949	29.4 (7)	28.3 (7)	Copulation occurring

DAILY BEHAVIOR

Voice: A number of different kinds of audible sounds are produced by pallid bats. Each of these seems to be associated with a particular type of behavior.

The "intimidation" note is a loud, strong, dry, insect-like buzz that is uttered when a bat is frightened, angered, or very annoyed. The

2. The fact that bats secured from this colony weighed more in the middle of April, 1951, than those secured about the same date in April, 1949, is attributed to their earlier seasonal appearance in 1951.

mouth is half-opened and the teeth bared at such times. From 1 to 7 successive buzzes may be given with equal time intervals between. The rate of utterance is about 3 to 5 per second. The individual buzzy notes are all of approximately the same pitch, quality, intensity, and duration. Any disturbance of a roosting colony during the day immediately resulted in one or more of the bats uttering this sound. Captive bats uttered the intimidation buzz when disturbed by persons attempting to handle them, when disturbed by other bats in the same cage, or when suddenly startled. This note was frequently uttered during the day by a female that was attempting to discourage her nearly grown young from nursing.

The "squabble" consists of a series of high-pitched, dry, rasping, thin, double notes of duration varying up to one second. In certain respects it resembles the squeaky note of the Anna hummingbird. This sound is produced with the mouth open and the teeth bared. Squabbling appeared to be a sign of irritability and anger and was uttered by individuals that were being crowded too much or slightly hurt by other bats. It was frequently heard during the day, especially when it was warm and the bats were restless. On several occasions the squabbling of pallid bats led to the discovery of colonies in the field.

The "directive" call usually consists of 1 to 5 rapidly repeated notes with equal time intervals between. The notes are single, clear, resonant in quality, and of a high pitch. They might be phonetically described as "sit" or "sit-sit-sit," depending on the number of notes uttered, and remind one of the sound made by a power line with a short circuit. This call is usually given as soon as a bat takes flight in the evening on emerging from a daytime roost. It was occasionally uttered by captive individuals when they were released for exercise in the laboratory. Captive bats were also heard to utter these notes sometimes while crawling about the laboratory or even when hanging in the room. This call is frequently heard at night in areas where pallid bats are abundant. On one occasion, in the midafternoon, 42 bats that had just been captured and examined were released one at a time close to their roost. The first 5 flew about for a few moments then entered a crevice in a rock. They uttered the directive notes after they disappeared from sight. These notes were answered by other bats, that were then released, and seemed to serve as a means of directing the latter to the same crevice. On another occasion, in the laboratory, it was noted that the utterance of directive notes by a bat 3½ months old caused 3 adults to fly to the young, hang next to it, and nuzzle it.

The directive note of the young pallid bats may be described as a "chirp." This is a high-pitched, bird-like note that the young are capable of uttering from the very moment of birth until they are

old enough to produce the adult type of directive note previously described. In captivity chirps were uttered as soon as a young bat became detached from its mother and were repeated monotonously until the parent rejoined the young. The frequency of utterance of these notes during periods of detachment increased from 2 or 3 per second during the first day of postnatal life to 5 per second by the tenth day. By the time young bats were about 12 days old this chirp was replaced by a directive call similar to that given by adults. In one instance this change in voice occurred at the age of 7 days. The chirp seemed to serve as a means of acquainting the female with the location of her young. When a female was separated from her young and released in another part of the room, or a young bat was taken from its mother and placed in another part of the room, the parent seemed to depend upon this sound to locate her offspring.

A sound which may be described as "chittering" was heard on some occasions. Although its significance is not clearly known, it was suspected of being a note of contentment. Each of these notes was of a high pitch, although the intensity varied slightly, of about one-half second duration, and repeated 3 or 4 times with half-second intervals between notes. On one occasion these chittering notes were heard coming from a cage in which an adult female and her 6-weeks old young were hanging side by side. Laboratory-reared bats that were very tame were occasionally heard uttering these notes during the daytime until they were 18 months old.

A "plaintive" note, presumably associated with pain, was uttered by females in labor. Such notes were high-pitched but not as high as the directive notes. They were loud, gutteral, harsh, double notes repeated 3 or 4 times, each note having a duration of about 2 seconds. They were uttered with the mouth open, the lips drawn back, and the eyes partly closed. They evoked no response from other bats in the same cage.

On occasion as bats groom themselves they produce a non-vocal, explosive, nasal sound. This apparently is the result of a sudden release of air through the nasal passages and may serve as a means of dislodging loose hairs that adhere to the nose.

When bats were flying about in a laboratory room they could be heard making faint clicks as they passed close by the observer. These same clicks were often produced by tame bats held in the hand at times when they were restless and about to take flight. The writer did not have an opportunity to study ultrasonic sounds produced by these bats but was kindly supplied with some information by Dr. F. Alton Everest of the Moody Institute of Science in Los Angeles. Through the cooperation of Mr. Eben McMillan 3 adult female and 3

nursing young pallid bats were secured by Dr. Everest at one of the colonies under observation by the writer on the Carrizo Plain. By means of an ultrasonic amplifier it was found that during flight these bats emit a very narrow beam of sound from the open mouth. The signal strength of this sound was found to fall very rapidly when the mouth was not aimed directly at the microphone. The same change in rate of click was observed as that described by Galambos and Griffin (1942). Pallid bats appeared to have an ultrasonic energy peak of about 40 kilocycles per second.

Locomotion: Pallid bats are capable of crawling quite well. When moving forward on a horizontal surface the weight of the body is borne on the wrists and feet. The knees are bent and directed upward and the tail is partly curled under. The fore part of the body is elevated more than the hind part. This position differs noticeably from that assumed by the Mexican free-tailed bat. Members of the latter species keep the body parallel to the surface on which they are crawling.

Figure 13. Pallid bat photographed at the moment it was taking flight from the edge of a table. Photographed at the California Academy of Sciences, October 26, 1952.

Figure 14. Shortly after the beginning of the downstroke. Photographed by Bob Lackenbach, September 1, 1949.

Figure 15. Position of wings in downstroke slightly later than shown in figure 14. Photographed at California Academy of Sciences, June 26, 1952.

Figure 16. Midway in the downstroke. Photographed at the California Academy of Sciences, December 10, 1952.

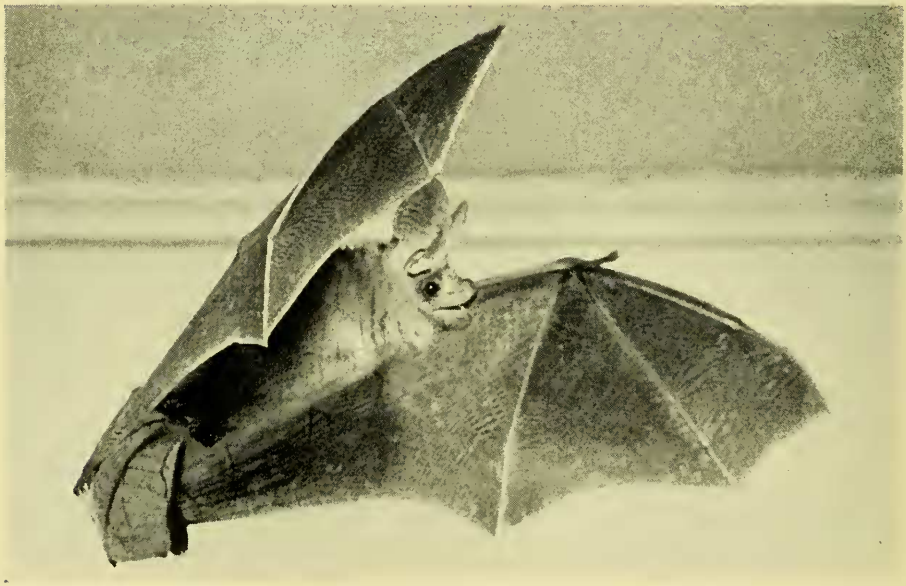


Figure 17. Near the end of the downstroke. Photographed by Bob Lackenbach, September 1, 1949.

Figure 18. At the end of the downstroke. Photographed at the California Academy of Sciences, November 20, 1952.

Pallid bats can climb readily, relying on the sharp claws of the hind toes and thumbs to hold on to vertical surfaces. If undisturbed when climbing they usually face the direction in which they are going. If they are bothered or frightened, however, they will frequently reverse their position and back up. No doubt this enables them to take flight more rapidly than would be possible if the head were facing upward. Likewise it generally makes it possible to direct intimidation notes and gestures more effectively toward the source of annoyance.

In flight, individuals of this species appear to be somewhat slower and less agile than many smaller bats. This impression results partly from the large size of the pallid bats. Their wing beats are slower and they require more room in which to turn. There is no question but that they lack the ability to maneuver in a limited space as effectively as smaller kinds of bats. It is questionable, however, whether they are actually slower flyers than most other vespertilionids. The Mexican free-tailed bat, on the other hand, which is a molossid with proportionately long, narrow wings, can outdistance the pallid bat very easily. Since these two species are frequently associated with one another, this was observed many times in the field as well as in the laboratory.

Field studies on flight under natural conditions were of little value as pallid bats emerge from their daytime roosts rather late in the eve-

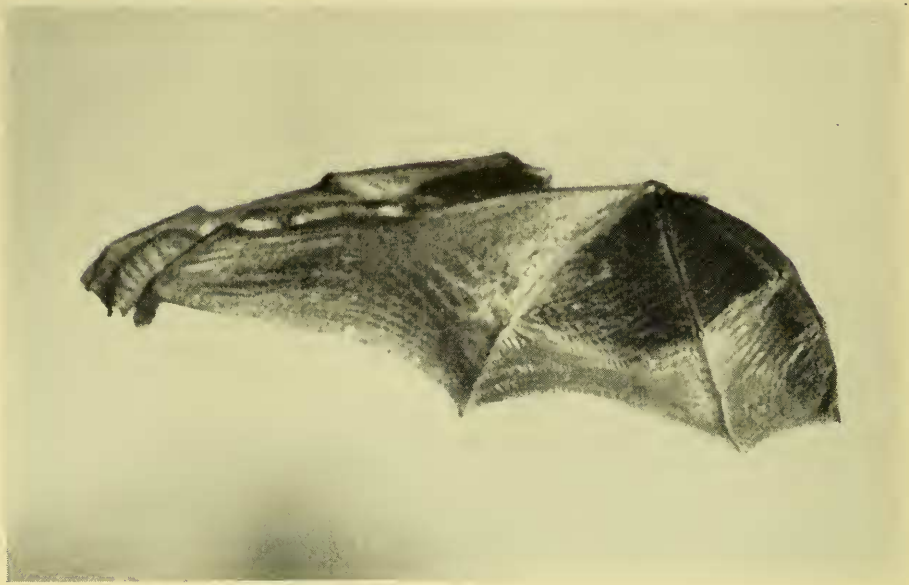


Figure 19. Midway in the upstroke as viewed from the side. Photographed at the California Academy of Sciences, November 20, 1952.

Figure 20. Midway in the upstroke as seen from below. Photographed at the California Academy of Sciences, November 20, 1952.

Figure 21. Near the end of the upstroke. Photographed at the California Academy of Sciences, April 29, 1953.

ning when the light intensity is very low. Studies, however, were made on the flight of captive bats in laboratory rooms. Direct observations were supplemented by slow motion films (64 frames per second) and stills made with a Speed Graphic and an Exacta VX using a Dormitzer Synctron electronic flash with a speed of about one five-thousandth of a second.

Before discussing the mechanics of flight it might be well to compare briefly a vespertilionid bat with a bird as regards the structures used in this form of locomotion. The chiropatagium may be considered as analogous to the outer half of a bird's wing. From the functional standpoint it serves the same purpose and acts as a propeller to effect forward progress. The plagiopatagium is analogous to the inner half of a bird's wing and like the latter serves to supply much of the necessary lift. The movement of the plagiopatagium is considerably less

than that of the chiropatagium in flight. The anterior part of the bat's wing, like the anterior part of a bird's wing, possesses the greatest rigidity and it is here that the drive or pressure is exerted on the downstroke. The uropatagium is analogous to the tail feathers of the bird and may perform many of the same functions.

On extending the wing of a bat it will be seen that the tension of the membranes is sufficient to cause the fourth and fifth digits to flex slightly so that the ventral surface of the wing is concave and the dorsal surface convex. The greatest bend occurs between the fifth metacarpal and the first phalanx of the fifth digit. The downward bend of the fourth finger is less pronounced. As will be seen in figure 16 the position of the hind leg and the pressure exerted by the air beneath the plagiopatagium serve to maintain this camber in flight.

Figures 13 to 21 illustrate the action of the bat's wing. The motion is essentially the same as that of the wing of a bird in forward flight (Aymar, 1935, pp. 136–137; Storer, 1948, pp. 31–32). The downstroke is downward and forward while the upstroke is upward and backward. This has already been noted by Griffin (1946) whose studies on flight were based upon high-speed photography developed by Professor Harold E. Edgerton at the Massachusetts Institute of Technology.

In one respect the upstroke may be considered less efficient in the bat's wing than in the bird's wing. In the bird the flight feathers of the wing can separate during this action to allow air to pass between them, thus minimizing resistance. No action comparable to this is possible in the bat. However, in the bat, as in the bird, resistance is minimized by the generally convex shape of the upper surface of the wing as well as by a partial folding of the wing during the upstroke. Slow motion pictures also show that the wing action is much more rapid on the upstroke than on the downstroke. Furthermore, on the downstroke the uropatagium is depressed considerably as a result of the legs being pushed forward and the tail curled ventrally (fig. 18). This tends to increase the lift in a species such as the pallid bat which has a large uropatagial membrane and thus partly compensates for the loss occurring with the succeeding upstroke. The uropatagium does not straighten out until the wings are raised.

The uropatagium not only aids in increasing lift during sustained flight but serves as a brake when a bat is slowing down to alight or to avoid an obstacle suddenly placed in its way. Under these circumstances the legs are separated more widely than in regular flight and thrust far forward, thus depressing the uropatagium. At such times the angle of the body and wings is increased so as to approach the stalling point.

While in flight the thumb is always extended, essentially at right

Figure 22. A close view of the head of a pallid bat in flight showing the position of the pinna, tragus, and mouth. Photographed at the California Academy of Sciences, November 20, 1952.

angles to the anterior edge of the wing. The mouth is opened slightly and the upper and lower lips are decidedly drawn apart anteriorly (fig. 22). This is believed to be associated with the utterance of ultrasonic sounds.

In the laboratory, pallid bats were occasionally seen to hover momentarily when flying close to the floor. At such times their forward progress was essentially stopped. Such hovering action was thought to be associated with the habit these bats have of capturing food on the ground. Occasionally pallid bats were observed to glide for short distances with the wings fully extended and up and down motion suspended or so slight as to be hardly discernible.

The number of wing beats per second was found to be subject to considerable variation, depending on the type of flight. Griffin (1946, p. 119) states that "Bats make about 15 strokes of the wing per second. . . ." This may be true of the vespertilionid bats of eastern United States that he studied. The pallid bat, which is considerably larger than any of the cave-dwelling species of eastern North America, was found to make 10 to 11 strokes per second in ordinary straight flight. The rate of wing beat was found to increase under certain circumstances, as for example in executing a turn. On such occasions as many as 13½ strokes per second

were recorded, while in a glide the number of strokes per second was reduced to zero for a brief period.

Pallid bats usually alight head up on vertical surfaces, catching on to the landing surface by means of the claws on their thumbs and hind feet. If the hind claws have found satisfactory crevices to cling to, the thumb holds are immediately released, as is also that of one hind foot. This causes the body to swing down to an inverted position at which time the claws of the thumbs and the released hind foot again grasp the landing surface. This method of alighting differs from that described by Dalquest (1947, p. 25), for *Corynorhinus rafinesquei,* a smaller and more agile species. It also differs decidedly from the way the phyllostomatid bat, *Macrotus californicus,* alights (Hatfield, 1937).

Odor: Pallid bats produce a very characteristic, skunk-like odor. On occasion one could detect this odor as much as 15 feet from an entrance to a roosting crevice. Disturbance of the bats results in a marked increase in the intensity of the odor. The odor is produced by the secretion of the glands on either side of the muzzle. On the surface of each gland are a number of pore-like depressions. A bristle is located in the center of each depression and each bristle is surrounded by about five smaller hairs (fig. 2). When a bat is disturbed, numerous tiny droplets of secretion are exuded within a few seconds and the odor becomes very strong. When the glands of a freshly killed bat are cut the odor becomes intense. It has been suggested that oil secreted by the nose glands of some bats is used to rub on the flight membranes to protect them from climatic conditions (Abdulali, 1949, p. 423). In the pallid bat, however, it seems more likely that the secretion may serve as a defense mechanism. It is true that members of this species frequently nuzzle their wing membranes but it is also true that the muzzle glands seem actively to secrete an odorous exudate only when the bats are alarmed. Perhaps this odor tends to repel certain other kinds of animals.

Diurnal behavior: Since the body temperature of many kinds of bats, including the species under discussion, has been found to be close to that of the environment when the animals are at rest during the day (fig. 23), it is not surprising that the behavior of these animals differs on cold days from that on warm days. On cool days, or early in the morning before it had warmed up, members of pallid bat colonies were found to be silent and essentially motionless until disturbed. If an individual was prodded at such times it would open its mouth and utter the intimidation buzz. Movement was slow at first and it was only after several minutes of continued disturbance that the bats would scramble around actively or be able to fly. On approaching a colony on a warm day one could frequently hear bats squabbling when 100 feet

Figure 23. Typical posture assumed by captive pallid bats when sleeping during the day. Photographed at the California Academy of Sciences, December 12, 1952.

away. Any attempt to reach into a crevice resulted in numerous intimidation and squabble notes as the bats actively backed to the innermost part of the roost. They were very alert at such times, keeping their heads raised and often their mouths open. The latter act was interpreted as an intimidation gesture. If further disturbed, various individuals would try to move rapidly to the roost entrance and take flight. Likewise, in the laboratory cages much more activity and quarreling were evident when it was warm than when it was cool.

Newly captured bats usually bit viciously when grabbed. Anger at other bats was often expressed by biting if the intimidation buzz failed to discourage the annoyer. This was often preceded or accompanied by

the squabble note. The majority of the bats that were kept in captivity for several months and handled regularly became accustomed to such treatment and ceased calling and biting when handled. However, they would usually open the mouth widely, bare the teeth, and occasionally move the jaws in a chewing sort of motion. Certain individuals never became tame while others became very tame. Some of the young born and reared in captivity would come of their own accord to the person that regularly cared for them and seemed to prefer being held in a hand to hanging in a cage. Bats that were wild or were being held in hand against their will would usually resort finally to spasmodic jerking of the body if all other means failed to give them freedom. Such behavior was frequently exhibited when body measurements or vaginal smears were being taken or when pelage examinations were being made. Such jerking ceased immediately when the animal was released.

During the day, captive bats were frequently observed nuzzling their fur and combing it with the hind claws. Whether or not the tongue was used in this cleaning process could not be determined. The flight membranes were also nuzzled and considerable time was devoted to scratching ectoparasites.

Captive pallid bats, both in laboratory and out-of-door cages, usually slept together in compact groups. Only occasionally would individuals stay apart from others in the cage and generally such behavior was the result of illness or injury. Not only did they customarily stay together but, after living in a cage a short while, developed the habit of roosting each day in the same place. When returned to a large flight cage after having been kept elsewhere for several weeks they would fly directly to the place where they had previously roosted. On several occasions roosts, consisting either of bricks or boards, were moved a few feet to determine the reaction of the bats upon being returned to a cage after an absence of two weeks. In each instance they flew to the original site of the roost and appeared bewildered. After a few moments of investigating, the new site of the roost was found. It was difficult to determine whether sight, odor, echo location, or all were involved in determining the position of the roosts.

On several occasions bats which had been captured in a barn in San Luis Obispo County were kept in San Francisco for as long as 13 months and then liberated at the original site of capture. Almost all of the bats, immediately upon being released outside of the barn in the daytime, flew directly to a small opening beneath the peak of the roof, that was regularly used by members of the colony as an exit and entrance to the attic of the barn where the roost was located.

Nocturnal behavior: Pallid bats do not emerge from their daytime roosts until fairly late in the evening. Observations made on June 8, 1948, on a colony in eastern San Luis Obispo County, showed that the first bats emerged 47 minutes after sunset at which time the illumination was less than 0.1 foot candles. By way of comparison, the first western pipistrelles were observed 2 minutes after sunset at which time the illumination was very high, and the first Mexican free-tailed bats emerged 17 minutes after sunset when the illumination was 3.0 foot candles. In the early morning of June 9, 1948, the last pallid bat was seen in flight 51 minutes before sunrise when the illumination was less than 0.1 foot candles. There is some evidence that in the fall of the year pallid bats, as well as several other species of bats observed, emerge earlier, relative to sunset, than in summer. On September 20, 1947, the first pallid bats were seen 19 minutes after sunset when the illumination was 0.15 foot candles. On that same evening western pipistrelle bats were seen 6 minutes before sunset and on the following evening Mexican free-tailed bats were seen emerging from daytime roosts 5 minutes before sunset. On this latter date, however, an overcast sky greatly reduced the amount of illumination. The earlier appearance of bats, in relation to sunset, in the autumn in the semiarid region where these observations were made may have been due to the scarcity of insect food at this season. Insects are less numerous in late September than in the middle of summer and less active after dark because of the cold. Certain other essentially crepuscular species of mammals, such as rabbits (Orr, 1940) are known to begin feeding activities much earlier in relation to sunset in winter when food is scarce than in summer when there is an abundance of palatable vegetation. Among diurnal birds Hinde (1952, p. 189) has shown that the great tit *(Parus major)* and the great spotted woodpecker *(Dendrocopos major)* roost later, relative to sunset, and emerge earlier, relative to sunrise, in midwinter than in autumn or spring.

Griffin and Welsh (1937) have shown that several species of insectivorous bats studied possess a definite activity rhythm, such as occurs in many other kinds of animals, and suggest (p. 342) that "Perhaps when the environment is constant, it is this internal mechanism that stimulates the animal at 24-hour intervals." No doubt this accounts for the rather uniform time of appearance of bats of the same species in the same region on a given date although seasonal changes in environmental conditions relating to food, temperature, and relative length of day and night undoubtedly affect the daily activity of bats in temperate regions.

On June 8, 1948, Mr. Eben McMillan, Mr. Ian McMillan, the writer, and his wife camped near a pallid bat colony along San Juan Creek in

San Luis Obispo County. From sunset that evening until after daybreak the following morning the entrances to the daytime roost and an adjacent night roost were kept under observation constantly by one or more members of the party. This was the second colony found on June 8, 1948, and has already been described on p. 181. At 7:30 P.M. a number of Mexican free-tailed bats were seen flying in and out of the cave in which the roost was located. The first pallid bat emerged at 8:00 P.M. During the next 15 minutes 4 more pallid bats emerged and during the next 5 minutes between 15 and 20 individuals made their exits. In each instance the lower opening of the cave was used. Each bat appeared to void urine a moment or so after emerging. On six occasions urine fell on a 10 by 12-foot tarpaulin located about 10 yards from the entrance to the cave and directly beneath the line of flight taken by the bats. After emerging from the cave each bat flew directly to the west about 50 yards where the ground level dropped abruptly about 20 feet to the creek. The bats upon reaching this point also dropped so that they were out of the observer's line of vision. It was suspected that the bats went directly to the creek to secure water but this was not determined. By 8:30 P.M., at which time it was nearly dark, some pallid bats were observed entering the night roost, which consisted of a shallow cavern in a cliff a few yards to the south of the daytime roost. During the remainder of the night bats were noted entering or leaving the night roost periodically. Sometimes quite a few individuals seemed to come at one time, sometimes they arrived singly in fairly rapid succession, and occasionally none would be noted for some minutes. Individuals approaching the night roost regularly uttered the directive call. Pallid bats were seen to enter the cave in which the daytime roost was located on only a very few occasions. At 11:00 P.M. 2 bats were found hanging from the roof of a small cavern about 30 feet north of the daytime retreat. At 12:30 A.M. about 8 or 10 pallid bats entered the main night roost and remained there until an observer approached with a flashlight at 1:10 A.M. All but two flew out. These remaining two were hanging from the roof of the cavern.

Between 1:57 A.M. and 3:00 A.M. an observer was stationed at the entrance to this night roost. A flashlight was occasionally used and there is little doubt that the presence of the observer disturbed the bats. However, a record was kept of the time and number of bats, whenever it was possible to determine the latter, that entered, as follows: 1:57 A.M., 1; 1:59 A.M., group; 2:01 A.M., 1; 2:02 A.M., 2; 2:04 A.M., 3; 2:07 A.M., 1; 2:09 A.M., group; 2:11 A.M., 3; 2:12 A.M., 1; 2:13 A.M., 2; 2:18 A.M., 2; 2:23 A.M., 2; 2:24 A.M., 1; 2:28 A.M., 12; 2:29 A.M., 2; 2:31 A.M., large group; observer left for 10 minutes to examine daytime roost and other night roost; 2:43 A.M., 1; 2:45 A.M., 1;

2:46 A.M., 1; 2:50 A.M., 1; 2:52 A.M., 2; 2:53 A.M., 1; 3:00 A.M., 1. It began to get light at 3:00 A.M. and from then on the number of bats seen decreased. The last pallid bat was seen flying near the entrance at 3:53 A.M. at which time it was fairly light. Investigation of the daytime roost at sunrise showed that it was deserted. Apparently the proximity of human beings during the night so disturbed the bats that they moved to an alternative roost, although the latter was not found by the observers.

The behavior pattern of the bats at this night roost conformed in general to that observed at other night roosts. Individuals came both singly and in groups. Frequently they would enter and seem to flutter momentarily against or hover near the wall of the cavern and then fly out. Occasionally individuals would alight. The time that they remained hanging varied from a few seconds to 40 minutes. It is probable that they often remain in a night roost for a considerably greater period of time than 40 minutes if undisturbed. Two other night roosts in natural caves were observed at night in addition to the roost observed on the night of June 8 and early morning of June 9. In most instances the bats observed hanging in these roosts were suspended by their feet from the center of the ceiling rather than hanging on the walls of the caves. As noted previously, however, this was not always true of bats using man-made structures for night roosts. Every pallid bat observed in a night roost was seen to be very alert and ready to take flight if alarmed. Nevertheless, by approaching slowly with a flashlight it was often possible to come within several feet of some individuals.

REPRODUCTION

In captive males enlargement of the gonads became noticeable toward the latter part of August. This was accompanied by a marked increase in the size of the cremaster sack which had been hardly apparent during May, June, and July. No pallid bats were examined in the field in August. Enlargement of the testes was evident in both captive males and those examined in the field in September. By the middle of October, however, there was a marked decrease in the size of the testes of both captive and wild individuals. Weekly examinations of four caged males from the middle of October, 1947, to the end of April, 1948, showed a steady decrease in the size of the cremaster sack. At the end of this time it presented the appearance of two darkly pigmented lines.

As has been noted by others who have studied the reproductive cycle of vespertilionid bats in the northern hemisphere, this decrease in the size of the cremaster sack in the fall is associated with a de-

crease in the size of the testes rather than the epididymes. As long ago as 1879 Fries described the prolonged retention of sperm in the epididymis of certain European bats of the families Vespertilionidae and Rhinolophidae and also noted that the accessory male reproductive glands were functional from fall until spring. Similar observations were made by Rollinat and Trouessart (1896). The first detailed histological studies of the male reproductive tract in the Microchiroptera were made by Courrier (1927) on *Pipistrellus pipistrellus*. Courrier not only confirmed the conclusions of earlier workers but also found that spermatogenesis occurs during the summer months. Miller (1939), working on *Myotis lucifugus* and *Myotis griseseens* in this country, found a similar seasonal sequence in the reproductive cycles of males of these species as have Pearson, Koford, and Pearson (1952) in *Corynorhinus rafinesqui*.

Although the gonads of male pallid bats have attained maximum size by late August and September, no evidence was obtained to indicate that copulation occurs before the latter part of October, by which time a definite decrease in size of the gonads has occurred. Vaginal smears from 29 females taken from a colony containing members of both sexes, in eastern San Luis Obispo County, on September 20, 1947, failed to reveal the presence of any sperm. Since no uterine examinations were made of these bats this cannot be considered as conclusive evidence that no copulation had occurred. However, the absence of spermatozoa in smears from such a large number of females makes it seem unlikely that many, if any, had been inseminated. On October 22, 1949, vaginal smears were taken from 7 females captured in the same region. Spermatozoa were found present in 2 of the females.

The spermatozoon of this species possesses a rather elongate, oval-shaped head which is truncate posteriorly. The body or connecting piece is of but slightly lesser diameter than the head. Its length is nearly half of the total length of the spermatozoon. Posteriorly it tapers to its junction with the tail piece. The total length of an average spermatozoon, measured with an ocular micrometer, was 36μ.

A number of observations were made on the breeding activities of pallid bats in captivity. On September 25, 1947, 3 males and 3 females that had been captured 5 days previously were placed together in an indoor laboratory flight cage where the temperature ranged from 50°F. to 65°F. These bats, as well as others that were later placed in this cage, were banded so that the activities of each individual could be followed. A few minutes were devoted to observation each morning and again in the afternoon when the bats were fed. Two of the males failed to show any signs of sexual activity during the succeeding six

months. These may have been young of the year although this could not be determined on the basis of external characters. Pearson, Koford, and Pearson (1952) have shown that it is improbable that the males of *Corynorhinus rafinesquei* copulate the first year. The third male was noted copulating with the same female on November 3, 18, 20, and 28. He was found copulating with the second female on November 9, and a vaginal smear taken from the third female on November 11 showed the presence of spermatozoa. The first female was permanently removed from the cage on December 5. The second and third females were removed on December 29 and replaced by two other females. On January 16, 1948, however, the second female was returned to the cage. The male was found copulating again with her on February 6, 13, and 16. She was removed to a separate cage on February 25, and on April 24 aborted two embryos. A vaginal smear taken on February 24 from one of the females placed in the breeding cage on December 29 revealed an abundance of spermatozoa, indicative of recent copulation. No signs of copulation were observed after this date.

Captive bats were observed to copulate both on the floor of the cage and while hanging upside down on the vertical screen walls. On all occasions the male lay over the back of the female but was never seen holding her with his mouth. The uropatagium of the female was pushed to one side at such times. All copulations were observed during daylight hours. No vaginal plug was ever found in the female although a jelly-like substance, rich in spermatozoa, was found in the vagina immediately after copulation.

To determine what effect out-of-door temperature might have upon the breeding activities of pallid bats in San Francisco, 3 females and a male were placed in an outdoor flight cage on September 25, 1947. These bats, like those kept in the indoor flight cage, had been captured 5 days earlier in eastern San Luis Obispo County. One of the females was observed copulating with the male on October 31, and on November 4, 5, 6, 10, 13, 14, 17, 18, 19, and 24. There were no indications that either of the other 2 females bred. A fourth female was placed in the cage on November 1 and was observed copulating with the male on November 12. No sexual activity was observed during December and on the 29th of that month the 4 females were removed and 3 other females were placed in with the male. There was no further indication of breeding, however, on the part of these bats during the succeeding months. The air temperatures, in degrees Fahrenheit, for San Francisco as compiled by the United States Department of Commerce, Weather Bureau, in the *Monthly Weather Review,* for October, 1947, to February, 1948, are shown as follows:

	Mean	Mean Maximum	Mean Minimum
October	62°	68°	56°
November	55.3°	61°	49°
December	51°	56°	46°
January	54.7°	62°	48°
February	50.8°	57°	45°

Summarizing these observations on the breeding of pallid bats in captivity, therefore, it would appear that those maintained in the indoor laboratory cage, where the extreme ranges in daily temperature were from 50°F. to 65°F., copulated during the months of November, December, January, and February. Bats kept in an outdoor flight cage in San Francisco bred only from the end of October to the end of November. The mean minimum temperatures for these two months were 56°F. and 49°F., respectively. There was no indication of breeding during December, January, and February when the mean minimum temperatures were 46°F., 48°F., and 45°F., respectively. None of the captive bats kept in this outside flight cage went into dormancy in the usual sense of the word as applied to colonial bats. They ate regularly during the winter and, on all except the coldest nights, appeared to be active.

Field observations failed to show that pallid bats breed in September. There is some evidence (cf. Seasonal Behavior) that the summer colonies break up in October. During this month and up until the middle of November these bats were found in smaller aggregations, in one instance just a pair, and in places where they were not observed in summer. Females with spermatozoa in the vaginal passage were examined on October 22. On the basis of these few facts, combined with those obtained from captive pallid bats kept in an outdoor cage in San Francisco, it would appear that in central California this species breeds at least in the latter part of October and in November.

Very little is known regarding the whereabouts, and nothing pertaining to the sexual behavior, of pallid bats in the wild during the months of December, January, February, and March. Certain North American species of colonial, vespertilionid bats that have been studied in winter have been found to show signs of periodic activity during the season of dormancy. This, as has been noted, was also true of captive pallid bats kept without food at temperatures ranging from 38°F. to 50°F. Possibly during these brief periods of activity copulation occasionally occurs. Pearson, Koford, and Pearson (1952) have shown

that in *Corynorhinus rafinesquei* in California copulation occurs mostly during the winter months. These authors also indicate that the males are much more active that the females at this season and probably copulate with the females while the latter are torpid.

The literature on this subject has been carefully summed up by Hartman (1933), Baker and Bird (1936), Wimsatt (1945), and others. With most vespertilionid bats occurring in the Northern Hemisphere copulation takes place principally in the fall of the year prior to hibernation. There may or may not be occasional copulations by bats aroused from dormancy during the winter, and again in spring just prior to or about the time of ovulation. *Miniopterus schreibersii,* which was studied by Courrier (1927) in France is, of course, an exception to this rule. In this species copulation and ovulation both occur in the fall. Fertilization takes place immediately and pregnancy lasts over the winter until spring. *Miniopterus australis,* studied by Baker and Bird (1936) in the New Hebrides, breeds in the spring at which time fertilization occurs. *Miniopterus* is considered exceptional in so far as the family Vespertilionidae is concerned. Bats of the family Rhinolophidae behave essentially like most of the Vespertilionidae in that they copulate in the fall of the year and ovulate in the spring. On the other hand, phyllostomatid bats (Hamlett, 1935) and molossid bats (Hartman and Cuyler, 1927; Sherman, 1937) that have been studied, copulate in the spring at the time of ovulation.

During this study an attempt was made to determine whether or not spring or late winter insemination is necessary, both for normal development and for fertilization, in the pallid bat. Guthrie and Jeffers (1938) induced ovulation in *Myotis lucifugus* in December and January by injections of hypophyseal extract and found that normal development did not follow, whereas ovulations induced in February were followed by normal cleavage and the formation of blastodermic vesicles. These authors, as well as Miller (1939) in his paper on the reproductive cycle of male bats, concluded that this difference in the activation reaction was conditioned by the introduction of fresh sperm during the late winter copulations. Pearson, Koford, and Pearson (1952, p. 299) conclude that in *Corynorhinus rafinesquei* "there is a refractory period during autumn and early winter during which ovulation does not normally occur. . . ." They further conclude "that ovulation is not readily induced by removing *Corynorhinus* from hibernation to warm rooms before mid-February, but that injections of pregnancy urine bring about ovulation at this time."

On December 5, 1947, a female pallid bat that had been captured on September 20, and was known to have copulated repeatedly during November, was removed from a cool room in which she had been

caged with a male and placed alone in a cage in a heated greenhouse where the temperature ranged from 75°F. to 78°F. It was hoped that this would induce ovulation. On February 26, 1948, she gave birth to one young which was reared successfully. The total elapsed time from the date on which the female had been placed in the warm room until parturition occurred was 83 days. Although the time of ovulation was not known, it is probable that some days elapsed between the time the bat was placed in a warm environment and the time of ovulation. Normal development apparently occurred in this instance in midwinter.

Wimsatt (1944) has shown that fall and early winter insemination can effect fertilization in the spring in *Myotis lucifugus* and *Eptesicus fuscus*. Ryberg (1947), apparently unaware of Wimsatt's (1944) work, mentions two instances in which females of *Nyctalus noctula* were captured in the fall after hibernation had commenced and kept cool and isolated during the winter. He states (p. 149) that "Long after they had awakened in the spring, they began, gradually, without any possibility of copulating again, to show signs of pregnancy."

To determine whether or not late winter or spring insemination is necessary for fertilization in the pallid bat, a female that was known to have copulated on November 12, 1947, and may have copulated subsequently, was isolated from all males in an outdoor flight cage on December 29, 1947. Sometime between the night of May 21 and the morning of May 24, 1948, she gave birth to one young. The young was dead when found on May 24, but appeared normal as regards development. Presumably, as often happens in captivity, the female deserted the young at birth and the latter died from neglect. Birth in this instance occurred nearly five months after the female was isolated from any males. As has already been indicated and will be shown subsequently, this greatly exceeds the gestation period of this species.

Vaginal smears were taken approximately once a week from 12 captive females, between December 4, 1947, and June 4, 1948, to determine whether or not any epithelial changes could be observed and correlated with the reproductive cycle. Between June and December, 1948, smears were taken once or twice a month. Small, sterile, rubber spatulas were used and each smear was diluted with a drop of Ringer's solution on a slide. The slides were examined with an 8 mm. objective and $\times 7$ ocular. Some of the bats used in the study were kept out-of-doors, others in a warm laboratory, and others in a refrigerated room during the winter and early spring of 1947–48, to see if environmental temperature had any effect.

In general it was found that squamous epithelial cells were present all year around. Although occasional cornified cells were noted during all months of the year, they were found in abundance from the end of

January until early in May. The greatest number of cornified cells, in proportion to nucleated epithelial cells, were observed in smears from bats kept at lower environmental temperatures. Leucocytes appeared in March and April, varying in time of appearance with the individual. There was no continuous invasion of the vagina by leucocytes during these months but rather a sudden rise and fall in the count. It was suspected that the appearance of leucocytes in numbers might be associated with ovulation, but this was not determined. An occasional leucocyte was found in early May, after which not one was seen. Guthrie (1933) noted large numbers of leucocytes in the vaginal passage in *Myotis lucifugus* at the time of ovulation in the spring.

As has previously been stated, a captive female that had bred was removed from a moderately cool environment and placed in a warm room on December 5, 1947. Eighty-three days later she gave birth to a normal young. It was believed that the increased temperature induced ovulation and that the gestation period may have been about eighty days, possibly less, depending upon the time required for the maturing of the follicle (see Guthrie and Jeffers, 1938). In order to further check the gestation period, 15 female pallid bats were secured on April 15, 1949, in eastern San Luis Obispo County. This was 5 days after the first appearance of bats at this colony site. They were transported to San Francisco and on the following day 4 were killed and their reproductive tracts fixed in Bouin's fluid. After this material was sectioned and stained it was found that one female had recently ovulated, possibly within 24 hours, although no tubal egg could be found. The ruptured follicular cavity had not as yet formed a corpus luteum. The three other reproductive tracts contained blastocysts in one or both horns of the uterus. In each instance implantation was beginning to occur on the antimesometrial side of the uterus and the beginnings of chorionic villi were evident on the side of the trophoblast next to the inner cell mass. A thin, single-celled layer of entoderm adhered to the underside of the inner cell mass and the inner surface of the trophoblast of each blastocyst. In one embryo the amniotic cavity had not as yet made its appearance. In each of the others a small amniotic cavity was present. In the most advanced embryo the flattened embryonic disc was quite apparent. To state the age of these embryos is a difficult matter. When compared with the macaque, studied by Heuser and Streeter (1941), which has a gestation period of 168 days, they are comparable to the development attained between the 9th and 12th days following ovulation. One would expect more rapid growth in the case of a mammal having a shorter gestation period. Guthrie and Jeffers (1938), however, found free uterine blastocysts in *Myotis lucifugus* at what was estimated to be the tenth day following ovulation

induced by injections of hypophyseal extract. If such slow development occurs in vespertilionid bats under natural conditions following normal ovulation in the spring, the most advanced embryos found in *Antrozous* females killed on April 16 might be estimated to be about 12 days of age. This would indicate that 3 of the 4 females ovulated sometime during the first week of April. Two more females were killed on May 2. One contained a single embryo, the other contained 3 embryos, 2 in the right horn of the uterus and 1 in the left. All 4 embryos appeared to be at about the same stage of development, but only 1 was removed from the foetal membranes for measurement. This individual had a crown-rump length of 5 mm. The others were preserved intact in their foetal membranes for future study. On May 18, 2 more females were killed. One contained 1, the other 2 embryos. Each embryo had a crown-rump measurement of 12 mm. On May 23 another female aborted 2 young. The first of these was eaten by the parent. The second dropped to the floor of the cage and was removed and preserved for later study. It measured 16 mm. from crown to rump. On June 1, one of the remaining 6 females showed obvious signs of illness and was found dead on June 6. A post-mortem examination indicated that she had probably died on June 4. One horn of the uterus contained an 18 mm. embryo. On June 7 two of the females gave birth to 2 normal young each. Another female produced 2 young between the evening of June 10 and the morning of June 13, another female gave birth to 1 young on June 14. The remaining female failed to produce young. Although she may not have been pregnant, there is the possibility that she aborted at some time without this fact being observed by the writer.

Thus, if we assume that the 4 females that gave birth to young between June 7 and 14 ovulated sometime between April 4 and 15, as was believed true of the 4 females killed on April 16, the possible maximum and minimum gestation periods would be 71 and 53 days respectively. It is reasonable to presume, however, that those that bore young first were the first to ovulate. This would indicate an average gestation period of about 9 weeks. However, Pearson, Koford, and Pearson (1952) as well as Eisentraut (1937) earlier, have suggested that environmental temperature, in so far as it affects the temperature of the mother, may influence the length of the gestation period in certain species of bats. Consequently it is possible that extended periods of cold weather in spring, during the time of pregnancy, may prolong the gestation period in this species.

Wimsatt (1945) estimated the gestation period for *Myotis lucifugus* to be between 50 and 60 days. Pearson, Koford, and Pearson (1952) indicate that in *Corynorhinus rafinesquei* the gestation period may vary

from 59 to 100 days, depending upon the mother's body temperature. Sherman's (1937) studies on *Tadarida cynocephala,* a molossid bat of the southeastern United States, led him to conclude that the gestation period in that species is between 11 and 12 weeks.

BIRTH AND GROWTH OF YOUNG

Number of young per female: Records of 28 females, from San Luis Obispo and Kern counties, that either bore young or were pregnant (4 captured with 2 young each, 10 gave birth to young in captivity, 14 had embryos *in utero*) are as follows: 1 female had 3 embryos, 20 females had 2 embryos or young each, 7 females had 1 embryo or young each. This is an average of 1.8 young per bearing female.

Hall (1946, p. 165) indicates that uterine examinations of 13 pregnant pallid bats taken in Nevada showed that 11 contained 2 embryos each, 1 contained 3 embryos, and 1 contained 1 embryo. Bailey (1936, p. 392) mentions 2 females taken in a cave in Nevada, each with 2 young attached. Burt (1934, p. 397) records 4 females taken at Indian Springs, Nevada, on the nights of June 2 and 7, 1929. Three of the females each contained a single, well-developed embryo and the other female contained 2 embryos measuring 22 mm. J. Grinnell (1914, p. 263) records a female taken along the Colorado River with 2 embryos. H. Grinnell (1918, pp. 352 and 356) records a female taken at San Bernardino, California, with 3 embryos and another taken at Painted Rock, San Luis Obispo County, California, with 2 embryos. Grinnell and Storer (1924, p. 61), on examining 19 females captured on May 27, 1915, at Snelling, Merced County, California, found that 15 contained 2 embryos each, 3 had 1 embryo each, and one was not pregnant.

Two young, therefore, appears to be the usual number borne annually by most female pallid bats. Occasionally there may be only one young and rarely three. It is difficult to understand how females of this species could successfully rear 3 young since they only possess 2 nipples and the young seem to hold tightly to these for the first few days after birth. It is possible that in females with 3 embryos one is resorbed prior to birth, although resorption of advanced embryos has quite justifiably been questioned by Ryberg (1947, p. 139).

Dates of birth: The time at which the young are born varies with individual females in the same colony and seemingly to some extent with locality and year.

On May 10, 1947, 7 female pallid bats were captured 2½ miles northwest of Carneros Spring in Kern County. Two had newly born young clinging to them and the remaining 5 were pregnant. The latter had all given birth to young in captivity by May 14. These were the

earliest seasonal field records for young obtained during this study. The region where these bats were found, however, was the hottest and most arid part of the entire area where observations were carried on.

On June 6, 1948, 10 pregnant females were captured at random from a colony 4½ miles northeast of Shandon, San Luis Obispo County. This locality was about 27 miles northwest of the site of the colony previously mentioned and was in a region that may be described as cooler and less arid in summer. Two of the females were prepared as study skins and each was found to contain 2 nearly full-term foetuses. The latter averaged 45.5 (45–46) mm. in total length and 2.55 (2.5–2.6) grams in weight. Four of the females were released 2 days later and the remaining 4 gave birth to young in captivity between June 14 and 23. On the evening of the same day the 10 pregnant females were captured, a lactating female pallid bat was shot near Carneros Spring in Kern County. It was thought that she had probably borne young several weeks previously. On the following day, June 7, 1948, 35 female pallid bats were taken from a colony on the northwestern edge of the Carrizo Plain, San Luis Obispo County. All were palpated before being released and were found to be in advanced stages of pregnancy.

Four females captured at the colony 4½ miles northeast of Shandon on April 15, 1949, gave birth to young in captivity between June 7 and 14. Two pregnant females were captured at this colony on April 14, 1951. One was killed on April 17 and found to contain 2 embryos with a crown-rump length of 7 mm. which indicated a much earlier ovulation date than was suspected for females taken from this same colony on April 16, 1949 (cf. table II). The second female was killed on May 25 and found to have 2 foetuses about ready for birth.

From the foregoing evidence, therefore, there is some indication that the time of parturition in eastern San Luis Obispo and Kern counties varies from year to year within the same colony. It is quite possible that early warm spring weather may be conducive to early seasonal appearance and ovulation. Within any one colony in this region such data as were gathered indicate that, in any one year, all the females bear their young within a period of several weeks.

On June 13, 1951, 10 young were secured from a colony of pallid bats inhabiting an attic at Stanford University, Santa Clara County, California. The smallest individual was about half grown and unable to fly. Its age was estimated at about 3½ weeks. Three others were about three-fourths grown but not quite able to fly. The remaining 6 had body measurements within the range of adults and could fly well. The oldest was believed to be about 6 weeks of age and probably was born the first week in May.

Regarding reproduction of this species in Nevada, Hall (1946, p.

165) may be quoted as follows: "It was noted that the embryos taken on May 17 measured only 3 mm. from crown to rump. The female taken on June 4, 6 miles south of St. Thomas, had two embryos nearly ready for birth, and the embryos found on June 7 at Indian Springs (Burt, 1934:397) also were nearly full term. On June 15, 1939, in crevices in the roof of a cave 10 miles west and 5 miles south of Fallon, Alcorn (MS) found about fifty females nearly every one of which had one or two young securely fastened to her mammae. Bailey (1936:392) found a colony of females with young in the same cave on June 27, 1927. The young of one female, he thought, were but one day old. Burt (1934:397) mentions young bats nearly full grown taken at Indian Springs on August 2 and 3; our specimen taken August 7, west of Lahontan Dam, is of similar age. It appears that young ordinarily are born in the first half of June."

Sex ratio of young: Fifty young comprising 25 taken at random from colonies in the wild, 21 born in captivity, and 4 removed from the uteri of pregnant females just prior to birth, were carefully examined to determine sex. Twenty-seven were males and 23 were females. These figures seem to indicate a nearly equal sex ratio at birth.

Parturition: The relatively meager literature on parturition in the Chiroptera has been fairly well summed up by Ramakrishna (1950). In general, breech presentation is characteristic of most of the species of Microchiroptera in which birth has been observed, exceptions having been noted in the case of *Nyctalus noctula* by Daniell (1834) and *Hipposideros speoris* by Ramakrishna (1950). Observations made on a number of captive pallid bats giving birth to young indicate that parturition in this species conforms in general to the pattern thought to be characteristic of the suborder.

During the period of labor and birth captive females hung upright. The uropatagium was curled ventrally at such times to form a basket and thus prevent the young from falling to the floor when born. The period of labor varied from a few minutes to nearly two hours. Females respired rapidly when in labor and frequently uttered notes of pain during contractions. When females had 2 young, the time recorded between the births varied from 12 to 65 minutes. All births observed were by breech. The rump and tail of the young, with uropatagium folded over the ventral part of the body, emerged first. As soon as the hind feet of the young were free they seemed to be used to further assist emergence by pushing against the mother's body. On several occasions a female was seen to sever the umbilical cord by biting it and later to eat the placenta when it was expelled. In most instances, however, the females were not under observation at times when this occurred. If the placenta was not found in the cage the following

day it was believed that the female had eaten it. Females that did not consume the placentae refused to accept their young and either killed the latter by biting them or else let them fall to the floor of the cage. The refusal of some captive females to accept their young was thought to be an abnormal condition associated with confinement in an artificial environment.

Females that behaved in what might be termed a normal manner licked their young frequently during the process of birth and then

Figure 24. Female pallid bat with young 2 days old. Photographed by Lionel T. Berryhill, May 15, 1947.

licked them thoroughly immediately after birth. One mother was seen to extend the wings of her newborn young with her mouth so that she could lick the membranes. Newly born bats seemed capable of climbing of their own accord to the mother's mammary glands. They used their thumbs, hind feet, and mouths to hold on to their mother's fur and pull themselves up. The female usually would assist by nuzzling the young. After a young bat became attached to its mother's nipple the female would envelop the young with her plagiopatagium so that the baby could no longer be seen. The young oriented itself in the same direction as the parent. Consequently, if she hung upside down the offspring did likewise.

Since young bats hold on very tightly to their mother's nipples (fig.

24) it is often very difficult to remove them to take body measurements. Furthermore, disturbance of this sort occasionally results in a female refusing to accept her young. Consequently, few newborn young were measured in captivity. However, the following selected measurements were made of two seemingly healthy young males a few hours after birth (figures in parentheses represent percentages of corresponding average adult male measurements): Total length, 48, 50 (42 per cent); tail length, 13, 15 (37 per cent); hind foot, 9, 10 (71 per cent); ear from notch, 8, 9 (30 per cent); forearm, 17, 18 (31 per cent). Their weights were 2.9 and 3.3 grams.

Development of young: At the time of birth young pallid bats have their eyes closed and their ears folded down tightly against the sides of the head. The skin of the body and the appendages is pink and to the unaided eye appears naked. When examined under a low-power microscope a few hairs will be found on the following parts: on either side of the head extending as a band from behind the rhinarium almost to the base of the antitragus, along the margin of the lower jaw, on the flight membranes immediately dorsal to the humerus and femur, and on the underside of the distal phalanges of the toes.

The information relating to growth of young given in the following paragraphs is based upon bats born and reared in captivity, unless otherwise stated (figs. 25 to 28). It is quite possible that under such circumstances the normal rate of growth and development may have been affected. A number of young developed malformations of the bones before maturity, presumably as a result of dietary deficiencies. Others seemed fairly normal.

By the fourth day of postnatal life the regions on which minute hairs could be detected had increased considerably so as to include an area extending from the tip of the tail anteriorly to the posterior lumbar region, then forward on either side of the body to the posterior thoracic area. Hairs also occurred on the dorsal surface of the legs and toes as well as on the wings from the thumb to the shoulder. These hairs could barely be seen by the naked eye at this time. By about the tenth day scanty fur was clearly evident on most of the upper parts of the body, excluding the area between the shoulders. Heaviest pelage was present on the lower back although the longest hairs were to be found on the posterior sides of the lower jaw.

The eyes, which were closed at time of birth, opened between the eighth and tenth days. The ears, although capable of being raised slightly by the third or fourth day, were not held erect until about the time the eyes opened. The tragus was pressed against the main body of the pinna thus closing the external auditory canal until this time.

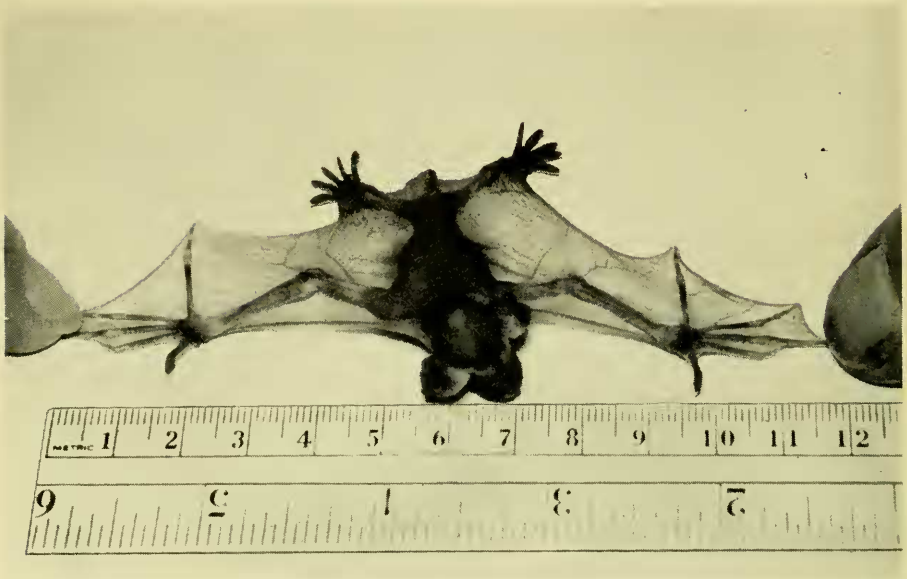


Figure 25. Dorsal view of a 3-day-old male pallid bat. Photographed by Lionel T. Berryhill, May 15, 1947.

Figure 26. Ventral view of a 3-day-old male pallid bat. Photographed by Lionel T. Berryhill, May 15, 1947.

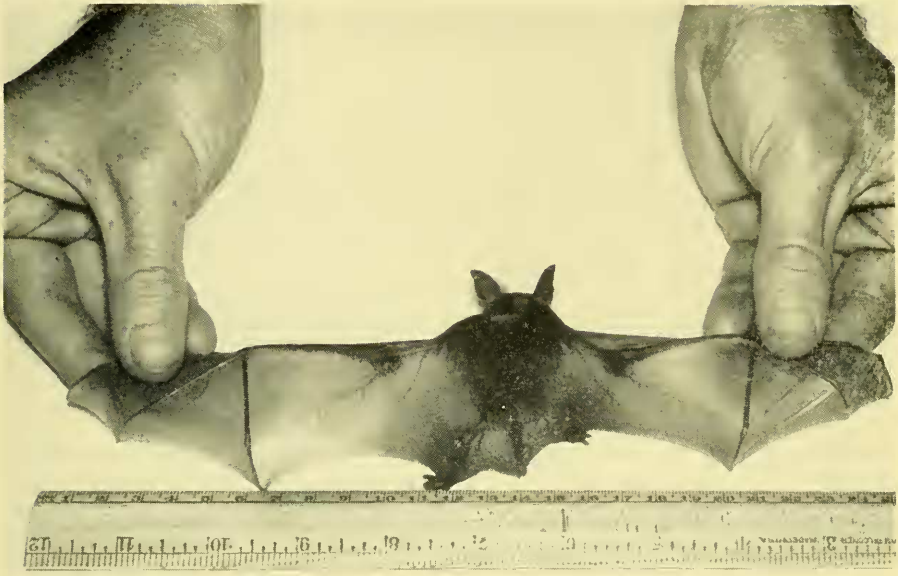


Figure 27. Dorsal view of a female pallid bat 30 days old. Photographed by Lionel T. Berryhill, June 9, 1947.

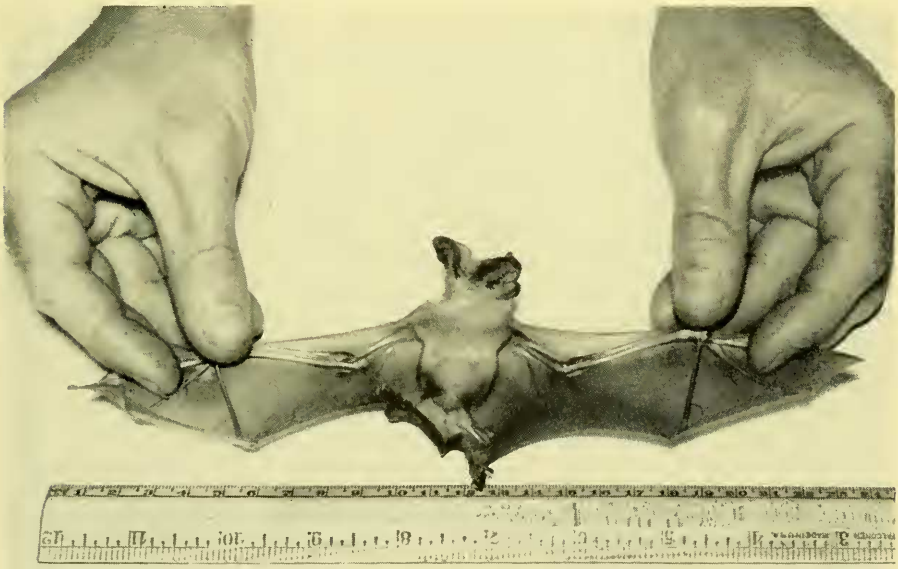


Figure 28. Ventral view of a female pallid bat 30 days old. Photographed by Lionel T. Berryhill, June 9, 1947.

Captive young were observed to exhibit fear when 10 days old. When a hand was placed near a young bat at this age it would draw back and utter an intimidation buzz.

Whether or not females in the wild carry their young with them when they forage at night was not determined. On several occasions females that were disturbed at their daytime roosts were observed flying away with their young attached. Griffin (1940, p. 182) states that "For the first three or four days after birth young of *Myotis lucifugus* are usually carried by the mother as she hunts." By the time young captive pallid bats were two weeks old they ceased hanging onto the mother during the daytime. The parent, however, kept the young beneath the plagiopatagium until they were too large for this arrangement and were forced to hang beside her.

By the eighteenth day a short, scanty pelage was seen on all of the upper parts of the body, except for the intershoulder area, and to a limited extent on the ventral parts. The skin, which was pink during the first week, had gradually darkened on the body wherever hair was present. The flight membranes had become somewhat grayish with the darkest coloration evident along the top of the tail and dorsal parts of the legs.

By the time the young were 24 days old the fur was sufficiently dense and long to obscure the skin except between the shoulders, a region relatively bare even in adults. At this age the general color of the dorsal pelage was much darker than that of adults. This resulted largely from the fact that only the darkly pigmented distal parts of the hairs had made their appearance and the light basal portions had not as yet grown out. The fur on the ventral parts of the body was a pale cream-buff, somewhat like that of the adult but with a more grayish cast. The flight membranes appeared vinaceous.

By the thirty-fourth day the light basal parts of the hairs of the dorsal parts of the body were evident. The young still appeared much darker than adults. Apart from the intershoulder area, which acquired a scanty growth of hair at 2½ months, pelage changes after the first month seemed only to involve increase in length of hairs.

The earliest age that a captive-born young was observed to fly was 7 weeks. However, wild-taken young whose measurements were approximately similar to captive young 6 weeks old were capable of flying quite well. It is significant perhaps in this regard to note that captive young began eating some mealworms by the time they were 6 weeks old, although they continued to nurse for several more weeks until the female would finally discourage this by keeping away from them or by threatening them when they came close to her.

The pelage of young when they have attained adult size is indis-

tinguishable from that of adults in new pelage. Many pallid bats were examined in the field in September and October. It seems highly probable that some of these must have been young of the year. If so, however, they could not be distinguished from adults at this season on the basis of external characters.

Tooth replacement: There is considerable variation in the deciduous dentition of the Chiroptera. Some bats, such as members of the family Rhinolophidae, possess deciduous teeth only in embryonic life. These teeth are reportedly absorbed prior to birth. Others retain their deciduous teeth for some weeks of postnatal life. In certain groups these teeth have the form of simple, straight spicules. In others they may be noticeably recurved. In some members of the family Vespertilionidae the deciduous teeth are not only recurved but may possess one or two accessory cusps.

The complete number of deciduous teeth in the pallid bat is 22, represented by the formula: i $\frac{2}{3}$, c $\frac{1}{1}$, pm $\frac{2}{2}$. As pointed out by Miller (1907, p. 20) this represents the maximum number known to occur in the order and is characteristic of a number of species of vespertilionids. In studying the sequence of appearance of the permanent teeth in this species the following material was used: 14 alcoholic specimens, ranging from foetuses nearly ready for birth to young 8 days old; 7 captive-born young whose dental development was followed from birth until the permanent dentition was acquired; 7 skulls of young whose approximate ages were determined on the basis of information derived from a study of young bats born and reared in captivity.

An examination of nearly full-term foetuses indicates that the first deciduous teeth to erupt through the gums are the upper and lower canines. Shortly following this the upper and lower incisors erupt, although in some specimens the first pair of upper incisors were somewhat slower than the others in appearing. This in general is the condition at time of birth, although Barrett-Hamilton (1910, p. 14) states that young bats, with the exception of members of the family Rhinolophidae, are born with complete deciduous dentition. The upper and lower premolars in *Antrozous* usually do not make their appearance until the third to the fifth day of postnatal life. In several newborn young, however, these teeth were in the process of breaking through the gums. By the early part of the second week the deciduous teeth are about fully grown out.

There is considerable individual variation in the shape of these teeth, especially the canines and premolars. The crowns of the upper and lower incisors possess a definitely trifid pattern with a main central cusp and two smaller accessory cusps, one on either side. The canines, both upper and lower, may vary from a condition in which three distinct

cusps are present to one in which only two cusps are faintly indicated. The upper premolars may be trifid, bifid, or have the crown more or less truncate in shape. The last form is most often seen in pm $\frac{2}{}$. Pm $\frac{}{1}$ is generally trifid while pm $\frac{}{2}$ varies like the upper premolars. The cusps, which are shaped like small hooklets, are curved inward. This is most pronounced, however, on the upper and lower incisors.

The deciduous dentition has long been considered to represent a primitive type of dentition. This was the contention of Winge (1941) and is a view generally held by mammalogists. However, with respect to the clasping type of deciduous teeth found in certain bats one must concur with Spillman (1927, p. 251) who describes this as a remarkable specialization not found in any other living or fossil groups of mammals. Such teeth unquestionably enable the young to hold tightly

Table III

Sequence of loss of deciduous teeth in *Antrozous pallidus*.

Upper teeth	*Age at which lost*	*Lower teeth*	*Age at which lost*
Pm^2	5 weeks	I_1	2–3 weeks
Pm^1	5–6 weeks	I_2	2–3 weeks
I^1	6–8 weeks	I_3	4 weeks
I^2	6–8 weeks	Pm_1	4 weeks
C	8–10 weeks	Pm_2	5–8 weeks
		C	8–9 weeks

Table IV

Order of appearance of permanent teeth in *Antrozous pallidus*.

Upper teeth	*Age at time of eruption*	*Lower teeth*	*Age at time of eruption*
C	4 weeks	C	3 weeks
I	4 weeks	I_1	4 weeks
		I_2	4 weeks
Pm	4 weeks	Pm_1	4 weeks
M^1	5 weeks	Pm_2	4 weeks
M^2	5 weeks	M_1	4 weeks
		M_2	5 weeks
M^3	5 weeks	M_3	5 weeks

to the mother's nipple when she is in flight. It is very difficult to remove young from the mother during the first week or two following birth without injuring the mouth of the former or the mammary gland of the latter.

The permanent dental formula for the pallid bat is: i $\frac{1}{2}$, c $\frac{1}{1}$, pm $\frac{1}{2}$, m $\frac{3}{3} = 28$. These teeth erupt through the gums internal to the deciduous teeth and for the most part their appearance precedes the loss of the deciduous teeth (tables III and IV). Certain of the latter teeth are present for some time after the young are weaned.

FOOD

Since pallid bats do not emerge from their daytime retreats until dusk it is difficult to make observations on their foraging habits. Some observers report that these bats go directly to water after taking to the air in the evening. Bailey (1936, p. 391), referring to members of this species, says: "At early dusk they begin to come out and usually fly directly to the nearest still water where they drink by repeatedly dipping to the surface, then begin their search for insect food." Nelson (1918, p. 493) makes the following statement regarding pallid bats: "Often when camping at desert waterholes, I have seen them come in just before dark to drink, scooping up water from the surface while in flight, and then circling back and forth over the damp ground at an elevation of a few yards for the capture of some of the insects common in such places."

Whether or not drinking water is essential for pallid bats is not known. However, only one of the summering colonies located during the course of this study was situated more than half a mile from known available fresh water. In this instance there was a spring 2½ miles away and it is possible that there may have been sources of water nearer. In captivity bats regularly drank water.

When foraging, members of this species generally fly fairly low and, as has long been known, frequently alight on the ground to capture food. Burt (1934, pp. 397–398) observed these bats usually flying 3 or 4 feet above the ground when foraging. He also records them frequently alighting on a lawn to capture June beetles *(Polyphylla)* in front of a ranch house at Indian Springs in southern Nevada during the summer. Nelson (1918, p. 493) reported the capture of a pallid bat that lit on the ground in an apple orchard in northern Arizona. The bat had caught a Jerusalem cricket *(Stenopelmatus fuscus)* and was so engrossed in its prey that it was readily picked up by the nape of the neck. Huey (1936, p. 285) records 2 pallid bats caught in mouse traps set for desert rodents in Mono County, California, on August 2,

1932. Since many insects, especially pinaeate beetles and desert crickets, had been observed coming to the bait the night before it was suspected that the bats had come to feed on the insects.

Nearly every pile of droppings beneath the day and night roosts of pallid bats examined during this study contained numerous remains of Jerusalem crickets which, of course, are flightless and must have been captured on the ground. The remains of scorpions were also frequently found in such places.

Mr. Eben McMillan, who contributed so much to this study, placed some clean grain sacks beneath some grain tanks where pallid bats were noted hanging up at night on the Pinole Ranch on the Carrizo Plain in San Luis Obispo County, on October 22, 1949. Each morning during the succeeding week the sacks were examined and then cleaned. On each of the first six mornings fresh remains of Jerusalem crickets were found beneath the roost.

On October 23, 1949, the writer found numerous insect remains beneath a pallid bat roost along San Juan Creek, 9 miles west of Simmler, San Luis Obispo County. Some of these were saved and later identified as parts of the following insects: Orthoptera: *Stenopelmatus* probably *fuscus;* Coleoptera: *Polyphylla* probably *decimlineata, Romaleum simplicicolle, Prionus californicus, Eleodes acuticauda.*

Mrs. Grinnell (1918, p. 355) records the remains of Jerusalem crickets and sphinx moths as being most numerous during the summer on the floor of a barn loft occupied by pallid bats at Glendora, Los Angeles County, California. A sample of insect remains dropped by these bats in this same loft in September contained parts of the following: Orthoptera: *Stenopelmatus* sp., *Microcentrum* sp., *Gryllus* sp.; Lepidoptera: *Deilephila* [*Celerio*] *lineata;* Coleoptera: *Prionus californicus, Ligyrus gibbosus.*

Hatt (1923, p. 261) lists the arthropod remains found with droppings beneath a pallid bat roost in September at Mission San Antonio de Padua, Monterey County, California. Most of these were Jerusalem crickets *(Stenopelmatus fuscus)* and scorpions *(Anuroctonus phaiodactylus).* A few other insect fragments identified included a grasshopper *(Schistocerca* sp.) and a beetle *(Polyphylla decimlineata).*

Borell (1942, p. 337) records the remains of grasshoppers *(Melanoplus differentialis* and *Schistocerca shoshoni),* large June bugs, and one large ground beetle, found beneath a night roost used by pallid bats near Albuquerque, New Mexico.

It is not known whether bats of this species regularly prey upon animals other than arthropods. Engler (1943, pp. 96–97), however, records captive pallid bats which were observed to eat western skinks *(Eumeces skiltonianus),* a Sonoran desert gecko *(Coleonyx variegatus),*

and were suspected of eating the head and neck of a Mexican free-tailed bat *(Tadarida mexicana)*. It seems likely that starvation was responsible for such deviation from an insectivorous diet, although, as the author suggests, it is possible that small night lizards may locally be preyed upon by pallid bats.

It is practically impossible to determine the quantity of food consumed nightly by insectivorous bats in the wild. In captivity, however, it is a relatively simple matter to ascertain the amount of food a bat consumes each night, although this does not necessarily represent the amount that would be taken under natural conditions. Mathias and Seguela (1940, pp. 15–19) found that *Myotis mystacinus* and *M. myotis,* fed on fly pupae, consumed an amount equal to about one-third of their own weight daily. Ramage (1947, p. 61) found that several species of *Myotis,* kept in small flight cages, ate about one-half their own weight in fly pupae or termites each night while a specimen of *Eptesicus fuscus,* kept in a small cage in which it could not fly, ate an amount equal to about one-third of its weight per day. As noted by that author the quantity of food eaten by captive bats varies greatly on different nights.

From May 25 to September 23, 1947, records were kept of the amount of food (meal worms in this instance) consumed by 3 captive pallid bats (1 male, 2 females) each night. The food was weighed before being placed in the cage each afternoon and the amount left in the morning was again weighed. From May 25 to August 13, the bats were kept indoors 41 per cent of the time. After this date they were constantly kept indoors. From May 25 to June 1 the average amount of food consumed per bat per night was 3.5 grams. The average weight per bat was 29.2 grams on June 5. During July the average amount of food consumed per bat per night was 4.2 grams. The average weight per bat was 29.9 grams on July 10. From August 1 to August 13, the nightly food consumption per bat was 4.5 grams. The average weight per bat was 28.3 grams on August 7. From August 14 to September 23 each bat ate an average of 4.7 grams of food per night. During this period, however, there was a marked increase in the weight of the bats. Their average weights on various dates were as follows: August 21, 30.6 grams; August 29, 32.3 grams; September 5, 33.5 grams; September 12, 35.1 grams; September 19, 38.6 grams. During this entire period of nearly 4 months these bats were given adequate amounts of food daily as evidenced by remains found in the mornings. The marked increase in weight during the latter part of August and in September may be attributed partly to lack of sufficient exercise, although there is evidence that under natural conditions bats show an increase in weight at this time of year.

While captive bats were principally fed meal worms during the early phases of this study and a prepared diet later (see p. 168) certain other kinds of animal food were occasionally offered them. They accepted the pupae of the following species of Diptera: *Lucilia sericata, Calliphora erythrocephala,* and *Calliphora vomitoria.* On one occasion an omnivorous looper moth *(Sabulodes caberata)* was accepted by a bat and eaten. On another occasion two of three snails *(Helix aspersa)* were eaten by captive pallid bats. California oak moths *(Phryganidia californica)* were refused.

No personal field observations were obtained relating to the manner in which these bats eat large insects. On several occasions, however, live Jerusalem crickets, held by forceps, were offered captive bats that were hanging head downward in cages. In each instance the bat viciously bit the insect, then reversed its position in the cage so that its head was uppermost. The tail and uropatagium were then curled up ventrally so as to form a basket before eating began. The position of the bat at such times was similar to that assumed by females when giving birth to young. The basket served to prevent the food falling to the ground until all desirable parts were consumed. The head and legs of these large crickets were discarded. Borell (1942, p. 337) observed a pallid bat in a similar position when it was eating a grasshopper, and Pittman (1924) described a similar posture for captive individuals of *Myotis lucifugus* when they were eating moths.

Parasites

The following ectoparasites were found on pallid bats from San Luis Obispo and Kern counties:

Hemiptera

Cimex pilosellus Horváth. Western bat bedbug.

Diptera

Basilia antrozoi (Townsend). Bat fly.

Siphonaptera

Myodopsylloides palposa (Rothschild). Flea.

Acarina

Ornithodoros stageri Cooley and Kohls. Tick.
Ornithodoros sp. Tick.
Spinturnix sp. Mite.
Steatonyssus sp. Mite.

Cimex pilosellus Horváth. On May 10, 1947, a western bat bedbug was found on a pallid bat captured at a daytime roost in western Kern County. On April 14, 1951, while trying to remove some pallid bats from a colony along San Juan Creek, 9 miles west of Simmler, San Luis Obispo County, a western bat bedbug was found adhering to a net which had been poked into the crevice housing the bats.

Basilia antrozoi (Townsend). This species of nycteribiid was found to be fairly common on pallid bats. Nearly all bats of this species examined during the spring and summer months had a few, usually 1 to 3, of these parasitic flies on them. The greatest number found on any one individual was 8. It is possible that these parasites are less numerous in the fall as only 10 out of 37 pallid bats captured on September 20, 1947, in San Luis Obispo County had flies on them. These insects showed a preference for the sides of the bodies of their hosts. They usually remained hidden in the fur unless disturbed. This species has previously been reported from *Antrozous* as well as from several other genera of the Family Vespertilionidae (cf. Stiles and Nolan, 1931, p. 648).

Myodopsylloides palposa (Rothschild). Fleas were found to be relatively uncommon parasites on pallid bats. They were recorded only three times and no more than one flea was ever found on a bat. Two specimens were collected on September 20, 1947, and another was secured on April 14, 1951.

Ornithodoros sp. Many pallid bats collected or examined in the field during the months of September and October were rather heavily infested with ticks. Those ticks collected during these months proved to be larval forms of the genus *Ornithodoros* but could not be identified as to species. A count was made of the number of ticks found on a group of 37 bats secured in San Luis Obispo County on September 20, 1947. Eleven of the bats were free of these parasites. The other 26 had the following numbers, respectively: 1, 1, 1, 1, 1, 1, 1, 1, 2, 2, 3, 3, 3, 3, 4, 4, 4, 4, 6, 6, 8, 10, 12, 13, 16, 26. Ticks were most frequently found on the sides and back of the neck, the shoulders, and sides of the body. Larval ticks were not found on the flight membranes.

On April 14, 1951, while capturing bats from a colony living beneath a loose slab of rock on a cliff 9 miles west of Simmler, San Luis Obispo County, a large number of adult ticks were found crawling up the perpendicular face of the cliff beneath the roost. In probing for the bats the ticks had apparently been dislodged and they were attempting to return to the crevice that housed the bats. A number of these were saved and proved to be *Ornithodoros stageri* Cooley and Kohls. An examination of 11 pallid bats captured here at this time revealed the presence of larval ticks on 5 individuals. The number of

ticks found on the bats varied from 1 to 11. A single adult tick of the above-mentioned species was found boring into the upper surface of the uropatagium of one bat.

Spinturnix sp., and *Steatonyssus* sp. Mites were commonly noted on the flight membranes of nearly all bats examined in the field and those kept in the laboratory. All those identified were either adults or nymphs of the genera *Spinturnix* or *Steatonyssus*. Individuals of the latter genus were generally more abundant than those of the former. The number of mites on pallid bats usually far exceeded that of all of the other ectoparasites together. No marked seasonal fluctuation in numbers was apparent.

Although no Diptera belonging to the family Streblidae were observed by the writer on any bats of this species, Jobling (1949) records *Trichobius corynorhini* Cockerell from *Antrozous* in California. This streblid primarily parasitizes bats of the genus *Corynorhinus* (cf. Kessel, 1952) but has been recorded on several other kinds of cave-inhabiting bats. Possibly the occurrences of these flies on bats other than those of the genus *Corynorhinus* is accidental.

Enemies

As was noted by the late Dr. Glover M. Allen (1939, p. 280), "Bats have few enemies." There is no indication that pallid bats are an exception to this rule. It is likely that their greatest enemy among the vertebrates is man who dislikes having small native mammals living in his attics and barns.

Pallid bats are occasionally preyed upon by owls. Baker (1953, p. 253) records the remains of 6 pallid bats found in pellets, belonging to either horned owls (*Bubo virginianus*) or barn owls (*Tyto alba*), collected in central Coahuila, Mexico.

Since bats of this species emerge rather late in the evening there is little likelihood of their being attacked by diurnal birds of prey under ordinary conditions. If a colony is subjected to occasional daytime disturbance, however, there is some evidence that individuals may be captured or at least harassed by small hawks. On June 9, 1948, 7 banded bats that had been captured 3 days previously at a colony about 30 miles away, were released at 7:00 A.M. close to a cliff bordering San Juan Creek in central eastern San Luis Obispo County. There were numerous crevices and small caves in the nearby cliff and several of the bats immediately flew to one of the recesses. Another lit on a sandstone outcrop and was immediately attacked by a Brewer blackbird (*Euphagus cyanocephalus*). It was able to avoid the attacker by scrambling into a narrow crevice. The other bats flew around

the cliff and disappeared from sight. Shortly afterwards, however, a sparrow hawk *(Falco sparverius)* flew over the cliff with an object that appeared to be a pallid bat in its claws. Another instance of a hawk attacking a bat of this species was observed about midday on October 23, 1949, at a rocky outcrop along the northwestern edge of Carrizo Plain in San Luis Obispo County. On this occasion while the writer and several others were attempting to capture a group of bats, found beneath a loose slab of sandstone, in order to band them, 2 individuals escaped. One of these was suddenly attacked, as it was flying about in the sunlight, by a sharp-shinned hawk *(Accipiter striatus)* that had been perched in a nearby oak. The bat evaded the hawk and dropped safely into a crevice out of sight.

Allen (1939, p. 288) mentions a record, supplied him by B. Patterson Bole, of a snake (species not known) that was found to have captured a pallid bat in California. As suggested by Allen it is not surprising that bats of this species, which occasionally alight on the ground, are sometimes caught by nocturnal snakes.

Hatt (1923, p. 261) in commenting on the remains of scorpions found beneath pallid bat roosts, a fact confirmed during the present study, makes the following comment: "It is difficult to understand how these bats capture the scorpions without being severely hurt or killed, for the venom of this scorpion is poisonous enough to kill most mammals of this size and the physical injury of the injection alone should be a serious matter to so small an animal. These scorpions are able to bend the postabdomen to such a wide range of positions that it would seem impossible that the bat could avoid being stung the greater number of times that it captured such prey. It is possible then that this bat is immune to the venom of a scorpion." Nothing is known regarding the immunity of pallid bats to scorpion venom or their ability to kill such arthropods without being stung. Consequently, the scorpion must be considered as a potential enemy until proved otherwise.

Summary

Pallid bats are to be found in colonies during the spring, summer, and early fall months. The number of individuals in established summer colonies observed during this study was found to vary from approximately 30 to 100. Daytime roosts may be in crevices in rocks or recesses in man-made structures, such as houses, barns, and bridges. Night roosts, where bats may rest or consume insects that they have captured, are usually close to the day roosts.

In central California pallid bats arrive at the summer colonies by the latter part of March or early April. Members of both sexes may

be present in a colony. The annual molt may occur any time between May and August. Summer colonies start to break up in October. During this month and early November the bats are found in smaller groups, often in situations where they are not to be seen earlier in the year. Little is known regarding the whereabouts of pallid bats in winter. They are absent from their summer retreats and have not been observed flying about at night. There is no evidence, however, that any extended migration occurs. The few records available of wintering individuals indicate that single bats or small groups pass the winter, probably in a torpid condition, in remote recesses. A study was made on the effect of lowered environmental temperatures on captive pallid bats. Individuals kept in a dark room without food for 144 days at temperatures ranging from 40°F. to 50°F. lost an average of 27.6 per cent in body weight or 0.193 per cent per day per bat. Bats kept under similar conditions but at temperatures between 38°F. and 40°F. for 119 days lost an average of 24.96 per cent in body weight or 0.209 per cent per day per bat. Bats kept for extended periods of time at low temperatures without food occasionally drank water and did not survive unless high relative humidity was maintained in their cages.

Seasonal fluctuations were apparent in the body weights of pallid bats. Lowest weights were recorded for bats when they first made their appearance in summer colonies in the spring. Males gained weight for several weeks, then maintained a fairly constant level until the end of summer. Females continued to gain weight until they had their young. Members of both sexes again showed an increase in weight in the fall.

Several kinds of vocal utterances are produced by pallid bats, including an intimidation note, a squabble, a directive call, chittering, and a plaintive note associated with pain. The odor, produced by glands on either side of the nose of these bats is distinctive and it is suggested that it may serve as a defense mechanism to repel other animals.

Studies were made on the flight of these bats, using slow motion pictures and stills made with the aid of an electronic flash. The motion of a bat's wing is essentially the same as that of a bird's wing in forward flight. The downstroke is downward and forward and the upstroke is upward and backward. The upstroke is considered to be less efficient in the bat's wing than in the bird's wing. The feathers of the latter can be separated to minimize air resistance at such times while any comparable action is impossible for the wing of a bat. Other actions on the part of a bat in flight, however, compensate for this loss in efficiency. In straight flight the pallid bat makes 10 to 11 wing strokes per second.

Members of this species emerge rather late in the evening. In early June the illumination was less than 0.1 foot candles when the bats emerged. In the latter part of September they were recorded emerging earlier in relation to sunset.

Observations in the field as well as on captive bats kept in outdoor cages indicate that in central California pallid bats copulate at least during the months of October and November. Copulation was observed in captive bats maintained in indoor laboratory cages between the months of November and February, inclusive. Nothing is known regarding the sexual behavior of these bats in the wild in winter.

Early winter ovulation was induced in a female that was placed in a warm room on December 5 and kept there until she gave birth to a normal young 83 days later on February 26. Another female that was known to have copulated was isolated in an out-of-door flight cage on December 29. Nearly 5 months later she gave birth to one young, showing that in this instance later winter or early spring insemination was not necessary for fertilization. Vaginal smears of captive females revealed the presence of nucleated epithelial cells all year around. Cornified cells were most abundant from the end of January until early in May. Leucocytes were noted only in March and April and their presence was thought to be associated with ovulation. The gestation period is estimated to average about 9 weeks. The average number of young for 28 females was 1.8. Young are born between early May and the middle of June, the time varying with year, locality, colony, and with individual females in a colony. The sex ratio at birth is nearly equal.

Females hang upright at time of parturition and the young are born by breech presentation. It would appear that under normal circumstances the female cuts the umbilical cord and eats the placenta. Young pallid bats have their eyes closed at birth and their ears are folded down tightly against the sides of the head. The body is essentially naked. The eyes open between the eighth and the tenth day of postnatal life, at which time the ears can be erected. Fear is exhibited by the tenth day. Fur is evident on parts of the body by the fourth day and has nearly grown out by the end of one month. Captive-born young were observed flying when 7 weeks old but it is believed that young in the wild can fly at an earlier age.

The deciduous incisors and canines have erupted through the gums at time of birth and the premolars generally make their appearance when the young are 3 to 5 days old. The first deciduous teeth to be lost are the premolars and the last are the canines. Many of the permanent teeth appear before their deciduous predecessors are lost.

Large orthopterous insects and beetles appear to be important in

the diet of pallid bats. Some of the insects eaten are flightless species which must be picked up from the ground.

Mites of the genera *Spinturnix* and *Steatonyssus*, ticks, and wingless dipterans belonging to the family Nycteribiidae are common ectoparasites on pallid bats. Less common are fleas and bat bedbugs. These bats have few known enemies. If disturbed enough to fly during the daytime they may be attacked by small hawks. There is one record of a pallid bat found in the stomach of a snake, and another of remains of pallid bats found in owl pellets.

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